INSIGHT INTO THE DIET HISTORY OF ICE SEALS USING ISOTOPIC SIGNATURES OF MUSCLE TISSUE AND CLAWS

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A

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Abstract

Climate change and sea ice reduction in the Arctic may impact foraging of ice-associated predators. The goal of my thesis work was to examine interannual differences in the diet of ringed, bearded, spotted, and ribbon seals as described by stable nitrogen and carbon isotope ratios of muscle tissue and claws to assess foraging plasticity. Isotopic mixing models from muscle data were used to describe the proportional contribution of prey groups during 2003, 2008–2010. Results showed a higher proportional contribution of smelt (Osmeridae) and benthic prey to ringed and bearded seal diets in 2003 compared to 2008–2010. Seasonal keratin layers deposited in claws can document trophic history up to about 10 years. During 2007 (record ice minimum), proportionally more ringed seals fed at a lower trophic level, while spotted seal adults and young-of-the-year fed at a lower trophic level during 2006. Bearded seals may have been foraging more pelagically from 2008 to 2010. Ice seals may be taking advantage of more abundant pelagic crustaceans as the Arctic ecosystem changes to a pelagic-dominated food web. Interannual variations and high variability among species and individual diets illustrate the opportunistic nature and flexibility of ice seals to changes in prey composition.

Dedication

To all those who believed in me . . .

My father who taught me determination ("Tiger in the Tank") and to strive for my dreams.

My mother who kept me believing I could accomplish anything. Her words gave me strength and reassurance.

My sister who kept reminding me that any big task can be finished by taking one step at a time. Our times of laughter lightened the load off my shoulders and uplifted me.

My grandfather who always thought of me as "a smart little cookie."

All my friends, especially Kim, Lorena, Carly, and Christy, who without their support I would be lost.

My husband, Chad, who was there for me every step of the way. It was a difficult journey having to be apart for a year after just getting married. His boundless patience, tremendous support, constant encouragement, and enduring love kept my feet running to the finish line.

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CHAPTER 1:

General Introduction

As the Arctic ecosystem changes so may the diet of Arctic pinniped species. An accelerated decrease in Arctic sea ice extent and thickness started in 2002 (Comiso 2006). Advection of warmer waters into the Arctic Ocean and continued loss of thicker multi-year ice resulted in 2007–2011 having the lowest September ice extents in satellite records since observations began in 1979 (NSIDC 2011). In response to continued sea-ice habitat loss and predicted reduced snow cover, bearded (*Erignathus barbatus*) and ringed seals (*Pusa hispida*) are proposed to be listed as threatened under the Endangered Species Act (NOAA 2011). Along with direct changes to habitat, Arctic pinniped species may be indirectly impacted by changes in primary productivity and distribution and abundance of prey sources in a changing Arctic. For instance, diminished sea ice, earlier ice melt, and warmer waters are thought to favor a pelagic-dominated food web (Bluhm and Gradinger 2008). An increase in pelagic grazers would reduce the export of organic carbon to the seafloor (Bluhm and Gradinger 2008) and over time this may decrease the benthic biomass (Dunton et al. 2005), possibly resulting in benthic consumers transitioning to foraging more pelagically. Dietary changes in prey composition have occurred for ice seals when comparing diets before and after the regime shift of 1976/1977 (Quakenbush et al. 2009, 2010a, b). In the 2000s, bearded seal stomachs consisted of more teleost species relative to the 1960s and 1970s, while benthic invertebrates, i.e., bivalves, became less prevalent (Quakenbush et al. 2010b). A switch to pelagic foraging by benthic specialists may increase competition for pelagic food sources (Bluhm and Gradinger

2008), which could be energetically costly to seals. Ultimately, a loss of sea ice may hinder foraging success of ice seals leading to a decrease in body condition, lower fecundity (Harwood et al. 2000), and eventual population declines (Simmonds and Isaac 2007). Thus, feeding ecology of ice seals should be examined on a temporal scale to document potential changes over time.

Stable isotope analysis has become a powerful tool to examine food-web structure and habitat use (Schell et al. 1989; Hobson and Welch 1992; Bentzen et al. 2007). For example, nitrogen exists in two forms as the lighter, more common stable isotope ^{14}N and as the heavier, less abundant stable isotope ^{15}N. Organisms preferentially use the lighter isotope for metabolic processes resulting in proportionally more of the heavier isotope being integrated into their tissues (Peterson and Fry 1987; Newsome et al. 2010). Stable nitrogen isotope ratios (expressed as $\delta^{15}N$ values) describe trophic position as the tissues of a consumer will be enriched in ^{15}N by about 3‰ compared to its prey source (Peterson and Fry 1987; Kelly 2000). Stable carbon isotope ratios (expressed as $\delta^{13}C$ values) have been used to illustrate carbon sources and habitat use (Schell et al. 1989; Dehn et al. 2007). For example, ice algae trapped in brine channels exhaust the available lighter isotope (^{12}C) and transition to using the heavier isotope (^{13}C) resulting in ice algae being more enriched in ^{13}C compared to phytoplankton that have more ^{12}C (Kennedy et al. 2002; Gradinger 2008). Thus, predators foraging on sea-ice-associated prey can have tissues more enriched in ^{13}C relative to pelagic foragers. Coupling stable nitrogen and carbon isotope ratios creates a distinct isotope signature for a predator that will vary based on the proportions of different prey items consumed. An advantage to using stable

isotopes is that they explain assimilated diet of a predator over an integrated period of time, which is dependent on the tissue examined, compared to stomach content analysis that depicts ingested prey during a snap shot in time.

Long-term feeding records for various marine and terrestrial mammals have been established using $\delta^{15}N$ and $\delta^{13}C$ values of keratinized and dentin structures (Schell et al. 1989; Hobson and Sease 1998; Darimont and Reimchen 2002). These tissues are metabolically inert and display the isotope signatures of the consumer diet at the time of deposition (Rubenstein and Hobson 2004). Annual diet information may be recorded in vibrissae as these structures grow continuously (Hirons et al. 2001; Cherel et al. 2009). Stable isotope ratios in vibrissae illustrate multi-year migration patterns and intra- and inter-individual variation in the diet of male Antarctic fur seals (*Arctocephalus gazella*) (Cherel et al. 2009). Whale baleen also provides a continuous long-term diet record and has been used to describe the annual migration of western Arctic bowhead whales (*Balaena mysticetus*) (Schell et al. 1989). Food sources in the Bering and Chukchi Seas are relatively enriched in ^{13}C compared to sources in the Beaufort Sea; thus migrations between the Beaufort Sea and the Bering and Chukchi Seas can be differentiated for marine mammals. A continuous long-term diet record is also captured in the dentin of teeth and the stable isotope ratios within these structures have been used to describe ontogenetic shifts in the diet of killer whales (*Orcinus orca*) (Newsome et al. 2009). Stable isotope analysis of tissues explaining long-term records provide a unique glimpse into the dietary history of individuals and over a sampled population.

The goal of my thesis work is to examine the dietary history of ringed, bearded, spotted (*Phoca largha*), and ribbon seals (*Histriophoca fasciata*) to assess potential interannual changes in the diets of ice seals. Dietary history is documented using $\delta^{15}N$ and $\delta^{13}C$ values in muscle tissue and claws. Isotope signatures within muscle tissue show integrated diet over several months or across a year depending on the size and metabolic rate of the animal (Tieszen et al. 1983; Sponheimer et al. 2006). Keratin layers, deposited annually in claws, can unveil dietary history up to 10 years (McLaren 1958). The first chapter of my thesis incorporates the isotope signatures of muscle into isotopic mixing models to describe the proportional contribution of prey guilds to the diet of ice seals during 2003, and 2008–2010. The second chapter investigates the feeding records within claws collected in 2007–2010 to illustrate interannual variations in the diets of individual seals and across the sampled population of each species. Comparing results from these two studies might present evidence of dietary shifts corresponding to recent climate change impacts on food-web structure. I hypothesize that during low ice years, bearded seals will forage more pelagically, while ringed and spotted seals will feed lower trophically compared to years prior to 2007.

CHAPTER 2:

Interannual Variations in the Diet of Ice Seals Assessed by Isotopic Mixing Models[1]

ABSTRACT

The Alaska Arctic is changing rapidly as sea ice thickness and extent decrease. Less sea ice may lead to alterations in productivity and food-web structure, leaving ice-dependent seals potentially vulnerable. We investigated the adaptation potential of bearded (*Erignathus barbatus*), spotted (*Phoca largha*), and ringed seals (*Pusa hispida*) by examining interannual differences in diet. Muscle was collected from seals harvested by Alaska Native subsistence hunters in 2003 and 2008–2010. Fish species of dietary importance to seals were sampled during cruises in the Chukchi Sea. Whole fish and seal muscle were analyzed for stable carbon and nitrogen isotope ratios. We used SIAR (Stable Isotope Analysis in R) to describe the proportional contribution of prey with distinct isotopic signatures to seal diets. Bearded seal diets had a higher contribution of benthic prey in 2003; this percentage decreased from 2008 to 2010. Spotted seals consumed a higher proportion of smelt in 2009, while ringed seals fed on a higher percentage of smelt in 2003 and 2010. Ice seals seem to be opportunistic predators and able to adapt to interannual changes in prey abundance, and thus are flexible to modifications in food-web assemblages associated with climate change in the Arctic.

[1] Carroll, S.S., Horstmann-Dehn, L., and Norcross, B.L. 2012. Interannual variations in the diet of ice seals assessed by isotopic mixing models. Prepared for submission to the Canadian Journal of Zoology.

INTRODUCTION

In the past few decades, average atmospheric temperatures in the Arctic have increased twice as fast as in the rest of the world (ACIA 2004). Rapid climate change is illustrated by the record minima of summer ice extent occurring in 2007–2010 (Perovich et al. 2010). Thus far, the 2011 sea ice extent was the second lowest ice extent since recording began in 1979, with 2007 having the record minimum sea ice extent (NSIDC 2011). There have been reductions in the extent and thickness of perennial ice in the Chukchi and Beaufort Seas since 1979 (Moline et al. 2008). Determining the responses of organisms to associated ecosystem changes will further the general understanding of adaptation potential and possible consequences for Arctic marine mammal populations to a warming climate.

Ice seals are dependent on sea ice as a resting, feeding, and pupping platform. In response to continued sea-ice habitat loss and reduced snow cover, the National Oceanic and Atmospheric Administration (NOAA) Fisheries Service is currently proposing to list the Pacific population of bearded seals (*Erignathus barbatus*) and the Arctic Basin population of ringed seals (*Pusa hispida*) as threatened under the Endangered Species Act (ESA) (NOAA 2010). NOAA decided in 2009 not to list the Bering Sea population of spotted seals (*Phoca largha*) under the ESA; however, the smaller southern population (Yellow Sea and Sea of Japan) was listed as threatened (NOAA 2009).

Diminished sea ice thickness and extent may increase energetic costs for many Arctic seal species. As the Arctic marine ecosystem changes with climate, so will the distribution and abundance of prey resources (Grebmeier et al. 2006). Lower nutritional

quality of prey could propagate up the food chain. This starts with essential fatty acids of ice algae being negatively correlated with increased irradiance due to reduced sea ice cover (Leu et al. 2010). Modifications to the food web as sea ice diminishes may lead to changes in seal diets, i.e., consumption of prey in reduced quantities or nutritional quality. Changes in prey quality, abundance, or distribution could lead to detrimental effects for ice seals, such as decreased body condition, impaired immune response (Burek et al. 2008), reduced fecundity (Harwood et al. 2000), and ultimately population declines (Simmonds and Isaac 2007). Thus, it is useful to examine the feeding ecology of ice seals on a temporal scale and document possible changes over time.

Stable carbon and nitrogen isotope ratios have been used to study food webs and identify likely dietary sources for Arctic species (Hobson and Welch 1992; Dehn et al. 2006; Bentzen et al. 2007). Stable nitrogen isotope ratios are indicative of the trophic level at which an individual feeds. As an organism consumes nutrients, it preferentially uses the lighter nitrogen isotope (^{14}N) for metabolic processes and integrates the heavier isotope (^{15}N) into tissues, leading to a stepwise enrichment of ^{15}N in the food web (e.g., Kelly 2000). Carbon-13 typically provides information on carbon source and habitat use, (e.g., benthic versus pelagic foraging, Dehn et al. 2007; Horstmann-Dehn et al. 2011). For example, benthic organisms rely on organic material from surface waters that ultimately undergoes bacterial remineralization, leading to tissues enriched in ^{13}C compared to pelagic organisms that consume fresh phytoplankton (McConnaughey and McRoy 1979). Ice algae trapped in brine channels exhibit similar ^{13}C enrichment

(Kennedy et al. 2002). Thus, predators that consume benthic organisms or ice-associated prey items have tissues more enriched in ^{13}C than those feeding pelagically.

An advantage to using stable isotopes in feeding ecology studies is that they provide dietary information over an integrated time period by reflecting assimilated, not just ingested food. Stable isotopes in muscle tissue describe integrated diet for gerbils (*Meriones unguiculatus*) over the previous couple of months (Tieszen et al. 1983). However, mass-specific metabolic rates of gerbils are faster than for large mammals, such as ice seals, thus tissues of larger animals have substantially slower turnover times. For example, the half-life of muscle (and associated stable carbon isotope signature) in alpaca (*Lama pacos*) is six times longer than that of gerbils (Sponheimer et al. 2006). Stable isotope ratios for muscle of large mammals thus describe long-term dietary averages of likely several months to a year (Sponheimer et al. 2006).

Isotopic mixing models have become powerful tools to evaluate predator diets and describe proportional consumption of prey (Phillips and Gregg 2001, 2003; Bentzen et al. 2007; Moore and Semmons 2008; Parnell et al. 2010). To make inferences about prey contribution to the diet of a predator, a comparison must be made between the isotopic signatures of the predator and its prey. Thus, three factors are inserted into mixing models: stable carbon and nitrogen isotope ratios of the predator and prey and a trophic enrichment factor. The trophic enrichment factor is the incremental change in stable isotope ratios from prey to predator tissues and is used to evaluate all food-web components in the same isotopic space (Peterson and Fry 1987). A key component to successful application of mixing models is distinct isotopic signatures of prey items

(Gannes et al. 1998). If prey signatures overlap, the model confounds the proportional contribution of each source (Phillips and Gregg 2003). Diet of a predator can be described using a single consumption percentage for each prey source if only two or three isotopically distinct prey items are eaten. However, many predators have a varied diet leading to a range of possible solutions for proportional contributions of prey items to the diet. Thus, as the number of food sources increases, the uncertainty to the particular contribution of each source increases as well (Phillips and Gregg 2003). Bayesian isotopic mixing models allow for the incorporation of more than two to three dietary sources and produce probable dietary solutions for each (Parnell et al. 2010). In addition, these models account for biological variability in stable carbon and nitrogen isotope ratios of predator and prey, and include measurement error (Parnell et al. 2010).

For this study, isotopic mixing models were used to describe the proportional contribution of prey sources to the diets of ice seals. To assess potential interannual changes in diet, stable isotope signatures within the muscle of bearded, spotted, and ringed seals were examined from 2003 and 2008–2010. Overall, diet analysis on a temporal scale may help to assess the foraging plasticity of these Arctic pinniped species.

MATERIALS AND METHODS

Seal Sampling

Muscle tissue of bearded, spotted, and ringed seals was collected during Alaska Native subsistence harvests in Barrow, Point Hope, Shishmaref, Little Diomede, and Hooper Bay (Figure 2.1). Bearded and ringed seals were sampled in May and June of 2008–2010. Spotted seals were sampled in October and September of 2008 and 2009. Ice

seals migrate long distances throughout marine waters in the Arctic and sub-Arctic (Kotzebue IRA and Arctic Web Publications 2010; Paulatuk Holman and Tyktoyaktuk Hunters and Trappers Committees 2011). Population structure of ice-associated seals is poorly understood and sub-populations may exist (Kelly et al. 2010). However, for the purposes of this study, individuals of their respective species were considered part of the same population although they come from different, geographically spread-out communities along the coastline in Alaska.

Seal muscle was collected shortly after death (less than 12 hours), placed in Ziploc® or Whirlpak™ bags, and frozen at –20 °C until processing for analysis of stable carbon and nitrogen isotope ratios. Approximately 5 mg of muscle was freeze dried (VirTis Sentry) for a minimum of 48 h and ground into a fine powder at the University of Alaska Fairbanks (UAF) Marine Mammal Laboratory. Seal muscle is typically lean, thus lipids were not removed from samples (Hoekstra et al. 2002). Some muscle samples were on tissue loan provided by the University of Alaska Museum of the North in Fairbanks (Loan # 2010.001.Mamm). These archived tissues were stored in 100% ethanol for two months prior to use. Ethanol preservation has been shown not to affect stable carbon and nitrogen isotope ratios of quail (*Coturnix coturnix japonica*) muscle (Hobson et al. 1997). As a comparison study, muscle tissue from five bearded and five ringed seals were analyzed as non-preserved and as preserved in 100% ethanol for two months. Stable carbon and nitrogen isotope ratios were not significant different between the two treatments of bearded seal muscle (for carbon: $p = 0.055$, $t = 2.68$; df = 4 and for nitrogen: $p = 0.231$, $t = 1.41$; df = 4) and between the two treatments of ringed seal

muscle (for carbon: $p = 0.302$, $t = 1.19$; df = 4 and for nitrogen: $p = 0.233$, $t = 1.40$; df = 4, respectively). Thus, for this study samples stored in ethanol were included in the analysis (Table 2.1). Muscle samples collected in 2008–2010 analyzed for this study were compared to seal muscle harvested during summer 2003 from the communities of Barrow, Shishmaref, Little Diomede, Savoonga, and Hooper Bay that were previously reported by Dehn et al. (2007) (Figure 2.1). Stable carbon and nitrogen isotope ratios of muscle samples from 399 seals were examined for this study (Table 2.1).

Seal teeth and front-flipper claws were used for age class classification. Jaws were soaked in hot water for approximately 15 min; teeth were extracted, carefully cleaned of gum tissue, and sent to Matson's Laboratory LLC in Montana for sectioning, mounting, and staining (Giemsa blood stain, Wohlbach formula, Ricca Chemical Company, Arlington, Texas, USA). Seal age was estimated by counting growth layer groups in the cementum of canine and postcanine teeth (Stewart et al. 1996), or by counting growth layer groups of claws for a minimum age estimate (McLaren 1958). One light and one dark growth layer is assumed per year in seal teeth and claws (McLaren 1958; Benjaminsen 1973; Stewart et al. 1996). Seals were assigned to one of three age classes: young-of-the-year (YOY), subadult (1–4 yr), and adult (≥ 5 yr) (Boveng et al. 2009; Cameron et al. 2010; Kelly et al. 2010)

Fish Sampling

Fish are common prey for ice seals and selected species were processed for stable carbon and nitrogen isotope ratios. Fishes were collected during research cruises in the Chukchi Sea. Demersal fishes were caught by bottom trawl during 2009 and pelagic

fishes were caught by surface trawl during 2007 (Norcross et al. 2011) (Figure 2.1). Fish species were chosen for stable carbon and nitrogen isotope analysis based on their frequency of occurrence in stomachs of ice seals (Quakenbush et al. 2009, 2010a, b) and their availability from research cruise collections. Twelve species of fish were analyzed: Arctic staghorn sculpin (*Gymnocanthus tricuspis*), Bering flounder (*Hippoglossoides robustus)*, polar eelpout (*Lycodes polaris*), shorthorn sculpin (*Myoxocephalus scorpius*), slender eelblenny (*Lumpenus fabricii*), stout eelblenny (*Anisarchus medius*), Arctic cod (*Boreogadus saida*), capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*), Pacific sand lance (*Ammodytes hexapterus*), rainbow smelt (*Osmerus mordax*), and saffron cod (*Eleginus gracilis*). For each fish species, stomachs were removed from ten individuals that were greater than 70 mm in total length for a separate study. Whole fishes without stomachs were freeze dried for a minimum of 48 h and homogenized using a mortar and pestle. Lipid content in fish tissues can alter stable carbon isotope ratios (Pinnegar and Polunin 1999). However, lipid extraction can also change stable nitrogen isotope ratios (Pinnegar and Polunin 1999; Sweeting et al. 2006). Therefore, fish samples were processed for lipid-extracted $^{13}C/^{12}C$ ratios and non-lipid-extracted $^{15}N/^{14}N$ ratios. Lipid was extracted from fish tissues using a modified technique described by Bligh and Dyer (1959). Dried, homogenized samples were immersed in a 2:1 chloroform:methanol mixture with a solvent volume about three times the sample volume (Logan et al. 2008). Each sample was agitated for five minutes followed by five minutes of centrifugation at 605 g (3000 rpm) using a VWR Clinical 50 centrifuge; the supernatant containing lipids was discarded. This process was repeated until the supernatant was colorless after

centrifugation (Logan et al. 2008), approximately three to five times. Lipid-extracted samples were dried overnight in a fume hood; freeze dried for approximately two hours the following day, and re-homogenized.

Stable Isotope Analysis

Seal muscle and whole fish were analyzed for their $\delta^{13}C$ and $\delta^{15}N$ values at the Alaska Stable Isotope Facility at UAF. A sub-sample of ground seal and fish tissue, 0.2–0.4 mg dry weight, was weighed into tin capsules using a micro-balance (Sartorius Model MP2).$\delta^{13}C$ and $\delta^{15}N$ values were determined using a Finnigan MAT Delta^{Plus}XP Isotope Ratio Mass Spectrometer (IRMS) directly coupled to a Costech Elemental Analyzer (ESC 4010). The $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios are expressed in conventional delta (δ) notation, relative to Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2 (atm.), respectively. Peptone was used as a laboratory-working standard. The precision of analyses, expressed as one standard deviation from multiple analyses of peptone (n = 63) conducted during runs of samples, was 0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Statistical Analysis and Isotopic Mixing Model

To identify potential correlations among age classes or sex, $\delta^{13}C$ and $\delta^{15}N$ values from analyses of seal muscle were examined statistically using cluster analysis. In addition, $\delta^{13}C$ and $\delta^{15}N$ values of muscle among the three ice seal species were analyzed using one-way ANOVA followed by Tukey's post-hoc test in R (Version 2.11.1, R Development Core Team 2011). For all statistical analyses, an alpha less than 0.05 was considered significant. The statistical package PRIMER 6.1.13 + PERMANOVA 1.0.3 (Anderson et al. 2008) was used to create a Bray-Curtis dissimilarity index and perform

cluster analysis. For the computation of the dissimilarity index, absolute value of $\delta^{13}C$ was used. Factors inserted into the program were age class, sex, and then age class and sex combined. In addition, $\delta^{15}N$ values were tested individually to investigate any confounding effects of young-of-the-year seals. YOY seals have been shown to display elevated $\delta^{15}N$ values in response to maternal nitrogen transfer via the placenta and nursing or increased metabolic demands during growth (Dehn et al. 2007). For each seal species no significant difference was found for age and sex across all years for muscle stable isotope ratios ($p > 0.05$). Therefore, all age classes and sexes were pooled to increase sample size and statistical precision, and stable isotope data for each seal species was then incorporated into stable isotope mixing models.

Model performance decreases when more prey items are included (Parnell et al. 2010); therefore, prey items were grouped into trophic guilds due to mixing model constraints. Seal prey were combined into trophic guilds based upon sharing similar isotopic space and their relative importance in seal diets (Phillips et al. 2005; Quakenbush et al. 2009, 2010a, b). Fish prey from Chukchi Sea collections were grouped as demersal or pelagic guilds (Table 2.2). Arctic cod is found throughout the water column and may be demersal or pelagic feeders (Cui 2009). For fish species, $\delta^{13}C$ (lipid-extracted) and $\delta^{15}N$ (non-lipid-extracted) values were analyzed using one-way ANOVA followed by Tukey's post-hoc test in R (Version 2.11.1, R Development Core Team 2011) to determine appropriate groupings. Based on isotopic data in this study, Arctic cod was part of the pelagic guild. Compared to Arctic cod and other fishes in this study, rainbow smelt was more depleted in ^{13}C ($p < 0.0001$, $F = 73.65$, $df = 11$) and was therefore

grouped in a guild by itself. Major guilds of invertebrate prey for ice seals consist of benthic decapods, mollusks and polychaetes, and planktonic crustaceans (Quakenbush et al. 2009, 2010a, b). A representative for each of these groupings was selected from the literature and used in the mixing model program. Benthic decapods were represented by the spider crab (*Hyas coarctatus,* Iken et al. 2010) for bearded seals and by common shrimp (*Crangon* spp., Iken et al. 2010) for spotted seals. Based on their isotopic signatures other decapod prey commonly consumed by seals that could be included in this guild are *Pandalus* spp. and *Chionoecetes* spp. (Gorbatenko et al. 2008; Iken et al. 2010; Feder et al. 2011). Greenland cockle (*Serripes groenlandicus,* Iken et al. 2010) is commonly consumed by bearded seals (Quakenbush et al. 2010a) and was selected as a representative prey item for the mollusk guild. Based on similar isotopic signatures other bivalves (e.g., *Macoma* spp.) or some polychaetes (e.g. *Nepthtys* spp.) could be represented in seal diets as well (Iken et al. 2010; Feder et al. 2011). The euphausiid *Thysanoessa rashii* (Iken unpublished[2]) was selected as a typical representative for the planktonic crustacean guild for spotted and ringed seals. Other planktonic crustaceans that share similar isotopic space with *Thysanoessa rashii* and are preyed upon by spotted and ringed seals are copepods and amphipods, such as *Calanus* spp. and *Themisto libellula* (Dehn et al. 2007; Quakenbush et al. 2009, 2010b; Iken et al. 2010; Feder et al. 2011).

The Bayesian isotopic mixing model, SIAR (Stable Isotope Analysis in R, Version 4.1.1, Parnell and Jackson 2011) was used to determine the relative proportions

[2] Katrin Iken. University of Alaska Fairbanks, Notification of unpublished data: November 2010.

of prey in seal diets. $\delta^{13}C$ and $\delta^{15}N$ values of seal muscle were grouped by year to document dietary proportions of the corresponding sampled population. Potential prey species of ice seals were grouped as previously described (Table 2.2) and their mean and standard deviation for $\delta^{13}C$ and $\delta^{15}N$ were inserted into SIAR. $\delta^{13}C$ and $\delta^{15}N$ values of prey items were adjusted to account for trophic enrichment factors for seal muscle, i.e., $1.3 \pm 0.4‰$ for $\delta^{13}C$ and $2.4 \pm 0.4‰$ for $\delta^{15}N$ (Hobson et al. 1996). $\delta^{13}C$ and $\delta^{15}N$ values inserted into the isotopic mixing models for prey were from a single year, whereas the values for ice seals came from four different years. Moreover, prey samples were not collected during the same season that the ice seals were harvested. For example, fish collections took place during August–September 2007 and 2009, bearded and ringed seals were collected during May–June 2003 and 2008–2010, and spotted seals were harvested during May–June 2003 and September–October 2008–2009. For the analysis, I used the available samples and this may have limited the accuracy of the mixing models as predator and prey tissues were not collected in the same season or year.

Tissue Turnover Calculation

Turnover rates for ice seals are unknown, but as a first approximation we calculated turnover in ice seals based on body size (body-size specific metabolic rates) from other mammals. A larger animal has a lower metabolic rate per unit weight compared to a smaller animal (Kleiber 1947) resulting in a slower turnover of tissues in the animal with the greater body mass (MacAvoy et al. 2006). For example, muscle turnover rates (half-life of carbon) for mice (*Mus musculus*), gerbils, alpacas, and steers (*Bos primigenius)* are 16.5 (MacAvoy et al. 2005), 27.6 (Tieszen et al. 1983), 178.7

(Sponheimer et al. 2006), and 151.0 days (Bahar et al. 2009), respectively. These experimental values were used to estimate muscle turnover rates for ice seals. Mass-specific metabolic rate is proportional to body size to the -0.25 power (West et al. 1997), a relationship which also applies to tissue turnover, i.e., half-life of ^{13}C = mass (in grams)$^{-0.25}$ (Carleton and Martínez del Rio 2005). Experimental values for the half-life of ^{13}C and mass $^{-0.25}$ for mice, gerbils, alpacas, and steers plotted on a logarithmic scale yielded a curvilinear regression (Figure 2.2).

[1] $$y = 180.15 - 369.35\ (x^{-0.25})$$

where x is the total body mass of the mammal in grams and y represents the half-life of isotopic incorporation in days. This agrees with published accounts as mass and metabolic rate, i.e., tissue turnover, have a convex curvature on a logarithmic scale (Kolokotrones et al. 2010). The regression equation from Figure 2.2 was used to estimate muscle turnover for an average-sized bearded, spotted, and ringed seal, i.e., 260,000 g, 90,000 g, and 45,000 g, respectively (Fedoseev 2000). Blubber mass should be considered when investigating mixing model results for muscle, as blubber is relatively inactive metabolically (Schmidt-Nielsen 1984), and may lead to an overestimation of turnover rate. Lean body mass was calculated using the LMD-index (length, mass, depth) to estimate percent blubber mass (Ryg et al. 1990) and this percentage was subtracted from the average body mass. For each species, standard length and body mass (Fedoseev 2000) were used for the LMD-index. Instead of using dorsal blubber thickness (Ryg et al. 1990), information was only available for sternal blubber thickness (Quakenbush et al.

2009, 2010a, b). In addition, blubber thickness varies seasonally and reaches its maximum in winter, thus winter averages were used (Quakenbush et al. 2009, 2010a, b). Due to limitations in available data, length, mass, and sternal blubber thickness during the winter season were used to calculate the lean body mass.

RESULTS

Based on average body mass, the half-life of isotopic incorporation for bearded, spotted, and ringed seals was 163.8, 158.8, and 154.8 days, respectively (Figure 2.2). Using lean body mass led to only minor differences in the half-life of isotopic incorporation for bearded, spotted, and ringed seals, i.e., 161.9, 154.3, and 150.2 days, respectively. Therefore, average total body mass was used to examine complete muscle turnover rates (doubled half-lives of isotopic incorporation). Complete muscle turnover rates for bearded, spotted, and ringed seals were approximately 10.9, 10.6, and 10.3 months, respectively.

$\delta^{13}C$ and $\delta^{15}N$ values of muscle (Figure 2.3) showed each seal species filling a distinct isotopic space. Muscle of bearded seals was significantly enriched in ^{13}C ($p < 0.0001$, $F = 50.75$, $df = 2$) compared to spotted or ringed seals (Table 2.1). Muscle of spotted seals had significantly higher $\delta^{15}N$ values ($p < 0.0001$, $F = 48.35$, $df = 2$) compared to bearded and ringed seals (Table 2.1).

Lipid versus non-lipid-extracted prey $\delta^{13}C$ and $\delta^{15}N$ values were compared to determine the effects on mixing models. Lipids did significantly influence fish stable carbon isotope ratios for all species ($p < 0.05$). For pelagic fishes, $\delta^{15}N$ values were significantly different after chemical lipid extraction (Arctic cod: $p = 0.0009$, $t = 4.86$;

capelin: $p = 0.0001$, $t = 6.39$; Pacific herring: $p = 0.0009$, $t = 4.83$; Pacific sand lance: $p < 0.0001$, $t = 7.34$; rainbow smelt: $p < 0.0001$, $t = 10.20$; saffron cod: $p = 0.003$, $t = 3.99$; df = 9 for all fishes). Thus, lipid-extracted $\delta^{13}C$ (carbon source rather than lipid signature is required for model performance) and non-lipid-extracted $\delta^{15}N$ (as indicator of trophic position) were used in SIAR. For benthic invertebrate prey, both non-lipid-extracted $\delta^{13}C$ and $\delta^{15}N$ were included in the mixing model (Iken et al. 2010). For pelagic invertebrate prey both lipid-extracted $\delta^{13}C$ and $\delta^{15}N$ values were used based on availability. Stable carbon isotope ratios of benthic invertebrates are not affected by lipid extraction in contrast to pelagic invertebrates (Iken et al. 2010).

Mixing model results illustrated demersal fishes, rainbow smelt, or both are key components to ice seal diets during the years sampled in this study. SIAR results are presented as upper and lower 95% credibility intervals (confidence intervals hereafter) for each prey source. For bearded seal diets, the highest possible proportion (i.e., upper 95% confidence interval) of demersal fishes was 58% in 2003, while in recent years the contribution declined to 45% (Figure 2.4, Table 2.3). In addition, the highest proportional contribution of pelagic fishes was lower in 2003, i.e., 35%, and increased in 2008–2010 to 44%–51%. Spotted seal diets had the highest contribution of smelt in 2009, i.e., 50%, compared to 2003 where smelt made up to 39% of their diet (Figure 2.4, Table 2.3). Ringed seals consumed a higher maximum contribution of smelt (Osmeridae) in 2003 and 2010 with 58% and 51%, respectively, compared to 2008 and 2009 with 41% and 44%, respectively (Figure 2.4, Table 2.3). Conversely, pelagic fishes and planktonic crustaceans were less prevalent in ringed seal diets in 2003 and 2010 than in 2008 and

2009 (Figure 2.4, Table 2.3). For all three seal species, confidence intervals overlapped for all proportional contributions of prey items and significant differences were not found for different prey groups across years (Payton et al. 2003; Julious 2004).

DISCUSSION

$\delta^{13}C$ and $\delta^{15}N$ values of muscle indicated that bearded, spotted, and ringed seals use different trophic niches. The relatively high $\delta^{13}C$ values of bearded seal muscle are consistent with benthic foraging (Dehn et al. 2007; Horstmann-Dehn et al. 2011). Bearded seals consume a variety of demersal fishes (e.g., cods, eelpouts, flatfishes, pricklebacks, and sculpins) and invertebrates (e.g., bivalves, crabs, and shrimps) (Cameron et al. 2010). Although, bearded seals may also eat pelagic fishes like capelin (Antonelis et al. 1994). The relatively high $\delta^{15}N$ values of spotted seal muscle suggest a diet reliant on fishes. Spotted seals consume both demersal and pelagic fishes that are also prey items for ringed and bearded seals (Boveng et al. 2009). Ringed seal muscle has a relatively depleted ^{15}N signature compared to spotted seals, indicating a mixed diet of pelagic fishes and lower trophic level pelagic crustaceans. Cods, euphausiids, amphipods, mysids, and shrimps are all important prey for ringed seals (Lowry et al. 1980a; Dehn et al. 2007). In general, these ice seal species feed on similar prey taxa; however, it is the proportions of prey consumed that create distinct isotope signatures of the different seal species.

Stable isotope mixing models can be used to detect interannual variations in foraging of ice seals. Muscle of bearded seals from 2003 and 2008–2010 represents averaged diet over approximately the previous 11 months (Figure 2.2). Isotopic mixing

model results indicate bearded seal diet consists of fewer benthic organisms and more pelagic fishes for 2003 compared to 2008–2010 (Figure 2.4). However, bearded seals focus foraging efforts on the benthos (Cameron et al. 2010). Declining sea ice and earlier ice melt is thought to result in a pelagic-dominated food web as ice-free waters expand (Bluhm and Gradinger 2008). When ice retreats earlier in the year, low light levels and little stratification delay the phytoplankton bloom. By the time the bloom develops, herbivorous zooplankton have become well established and consume much of the phytoplankton. This leads to decreased carbon flux to the benthos and reduced benthic productivity (Bluhm and Gradinger 2008). Mixing model results in this study provide evidence that bearded seals could be able to adjust to less benthic biomass by foraging on pelagic prey sources during ice minima years of 2008–2010 (NSIDC 2011). Fishes are considered of relatively minor importance to bearded seal diets (Lowry et al. 1980b). Mixing model results show benthic fishes and crabs as a large contributor to their diet and conversely to published accounts (Johnson et al. 1966; Lowry et al. 1980b), bivalves are of comparatively minor significance. This may be a response to niche competition with other predators. Walruses (*Odobenus rosmarus divergens*) largely depend on clams as a prey resource (Lowry et al. 1980b). Increased competition or low abundance of clams, possibly in accordance with reduced sea ice and walruses exhibiting a central foraging strategy from shore (Sheffield and Grebmeier 2009), could put pressure on bearded seals and effectively change their foraging efforts (Lowry et al. 1980b). However, as mentioned before, stable isotope results of muscle are an integrated, long-

term descriptor of diet and seasonal importance of bivalves as bearded seal prey cannot be ruled out.

Rainbow smelt, demersal fishes, and shrimps appear to be key resources for spotted seals, with seals harvested in 2009 having the highest contribution of smelt in their diet compared to 2003 and 2008 (Figure 2.4). Differences in diet among the years examined may be a result of the amount of feeding in nearshore habitats. All seals were harvested nearshore by subsistence hunters; however, seals could be feeding farther offshore during some part of the year prior to being harvested. The distribution of spotted seals has been documented by satellite tracking (Lowry et al. 1998). Spotted seals are typically found on ice floes near the ice front in late winter/spring, and as the ice breaks up they either move to nearshore haulouts in the Bering Sea or travel north into the Chukchi Sea from summer to early autumn (Lowry et al. 1998). During the open water season, spotted seals spend long time periods at sea and make infrequent visits to coastal haulouts (Lowry et al. 1998). Haulout locations for spotted seals in Alaska are located near spawning areas for pelagic fishes, i.e., herring, capelin, and smelt (Quakenbush 1988). Diet as described by stable isotopes of spotted seal muscle averages over approximately the previous 10.5 months (Figure 2.2). The higher proportional contribution of smelt in the diet of spotted seals harvested in 2009 may be the result of spending more time foraging nearshore compared to the seals collected in 2003 and 2008 (Figure 2.4).

Rainbow smelt and demersal fishes are more prominent in the diet of ringed seals harvested in 2003 and 2010 (Figure 2.4) likely relating to a higher abundance of these

fishes in those years. Rainbow smelt spawn in most major rivers draining into the Bering, Chukchi, and Beaufort Seas (Haldorson and Craig 1984). When this anadromous species migrates to nearshore waters in autumn and winter, it can be a dominant winter fish species in these waters (Haldorson and Craig 1984). Ringed seals may be taking advantage of this abundant resource when nearshore. Ringed seals were harvested in May/June and their muscle signatures provide dietary information averaged from about the previous 10 months (Figure 2.2), i.e., approximately August 2002–May 2003. From 2001 to 2003, the abundance of rainbow smelt and Arctic flounder (*Pleuronectes glacialis*) reached high catch rates in Prudhoe Bay, possibly as a result of higher than average west winds during summer 2002 (Fechhelm et al. 2004). The prevailing easterly winds give rise to upwelling conditions (Pickart et al. 2009), while west winds promote downwelling. Downwelling could move eggs and larval fishes towards shore and may have led to increased recruitment of rainbow smelt and benthic fishes. It is not known if rainbow smelt and demersal fishes were more abundant in 2010 compared to 2008 and 2009. Abundance and distribution of Arctic fishes are poorly documented (Johnson et al. 2010) and annual trends are therefore difficult to compare. Arctic cod is a dominant prey item for ringed seals during ice-covered years, while invertebrates become more important during the open-water season (Kelly et al. 2010). Mixing model results for ringed seals provide further evidence of a mixed fish and pelagic crustacean diet (Figure 2.4). Shrimps have been documented as an important food item for ringed seals (Lowry et al. 1980a), and the isotopic group of demersal fishes could also be indicative of shrimps because these taxa are close in isotopic space (Table 2.2). Ultimately, stable carbon and

nitrogen isotope ratios in muscle provide evidence that ice seals may be capitalizing on the more abundant prey sources (Dehn et al. 2007).

A comparison of the diets among ice seal species is perplexing as mixing model results were somewhat contradictory. Bearded seals fed on a lower proportion of demersal fishes in 2010 compared to previous years, while ringed seals had a higher contribution of demersal fishes to diet in 2010 (Figure 2.4). In addition, spotted seals fed on a higher proportion of smelt in 2009; whereas, ringed seals consumed more smelt in 2003 (Figure 2.4). These contrasting results could relate to distribution of each seal species or local variations in food sources. For instance, the northern range distribution of spotted seals is Point Barrow (Boveng et al. 2009), meaning they are rarely found in the Beaufort Sea. It is uncertain if the abundance of rainbow smelt found in Prudhoe Bay in 2002–2003 (Fechhelm et al. 2004) extended into the Chukchi and Bering Seas. Further studies to document the distribution and abundance of fishes in these seas over time would enhance the ability to link prey to their higher trophic predators.

Ice seals are opportunistic predators and most likely will conserve energy and consume abundant prey sources regardless of moderate differences in caloric value. Energetic density of dietary lipids is over twice that of carbohydrates and proteins (Schmidt-Nielsen 1997). Lipid content of rainbow smelt and flatfishes is almost twice that of Arctic cod, but is considerably lower than capelin, i.e., 8.7%, 7.9%, 4.5%, and 24.3%, respectively (Anthony et al. 2000; Ball et al. 2007). Generally, pelagic fishes have higher caloric values (based on dry weight) relative to demersal fishes (Ball et al. 2007), e.g., 20.5 cal g^{-1} for capelin and 16.5 cal g^{-1} for flatfishes (Anthony et al. 2000). More

specifically, nearshore demersal fishes have intermediate energy densities, while schooling pelagic fishes have either relatively high or low caloric value, and this is directly related to their lipid content (Anthony et al. 2000). Lipid content varies for fishes with regard to size, sex, reproductive status, month, year, and location (Anthony et al. 2000). Lipid-rich prey are good sources of energy if they can be digested properly. The higher lipid content of capelin compared to herring actually results in lower assimilation efficiency in seal guts (Lawson et al. 1997a). Ultimately, ice seals demonstrate preferential feeding but will eat what is available if necessary (Lindstrøm et al. 1998). Energy spent traveling to foraging grounds may lead to depletion of blubber stores and thickness, resulting in a potential increase of energy needed to augment insulation losses (Rosen et al. 2007). Instead of searching long distances for more energy dense food items, piscivorous predators can gain more energy consuming a plentiful resource of potentially lower quality. Ice seals preferentially feed on prey items that are numerous. For example, during spring 1981 bearded seal stomachs from the Bering Sea showed a high frequency of occurrence of capelin due to presence of dense schools around St. Matthew Island (Antonelis et al.1994). Similarly, regional differences in the diet of spotted seals were correlated to abundance and seasonal distribution of their food source (Bukhtiyarov et al. 1984). Mixing model results from this study provide further evidence of interannual differences in the diets of ice seals that most likely are on account of abundant prey sources.

Stable isotope and mixing model analysis provides an integrated view of diet and highlights important annual prey sources, although some important limitations and

assumptions need to be recognized. The results of the isotopic mixing models had limitations due to sample availability. Because the prey samples only came from a single year, I assumed that stable isotope signatures of prey did not vary interannually. Due to the timing of subsistence harvests and research cruises, the majority of ice seal samples and their prey did not come from the same season; therefore, variation within years is not accounted for in the isotopic mixing models. However, this initial examination using isotopic mixing models is still beneficial as a starting point to assess potential interannual changes in the diet of ice seals. Stable isotope turnover and integration into muscle tissue are poorly understood for marine mammals. This study extrapolated a tissue turnover rate for marine mammals based on experimental results from terrestrial mammals. In addition, tissue turnover can be difficult to assess for animals changing diets seasonally. Care should be taken when interpreting mixing model results and isotope values of all potential prey items need to be scrutinized, especially for predators with a varied diet. For example, mixing model results for spotted seals show demersal fishes and shrimps having a high contribution to their diet, but the confidence interval is wide (Figure 2.4). Further confounding factors complicating mixing model analyses are variable metabolic rates based on gender, age, season, and nutritional and physiological state of the animal. Breeding males, lactating females, and young seals are likely to have different metabolic rates and tissue turnover rates, e.g., younger animals have higher metabolic demands than older seals due to enhanced growth rates (Newsome et al. 2010). Moreover, starving animals have tissues enriched in ^{15}N (Hobson et al. 1993). In contrast to terrestrial mammals, marine mammals will not catabolize protein during sometimes extensive

fasting periods. However, during times of starvation, marine mammals no longer refrain from protein sparing and begin to breakdown lean tissue mass (Castellini and Rea 1992). The excreted ^{14}N is not being restored by dietary protein and the animal is essentially feeding on itself, thus leading to an enrichment of ^{15}N in tissues (Gannes et al. 1997). This could lead to biased results and misinterpretations in the apportionment of prey to dietary proportions. The composition of protein and lipids within a prey item can also influence stable carbon and nitrogen ratios assimilated into predator tissues. Seals alter their assimilation routes to adjust for differing macronutrient composition of prey (Zhao et al. 2006a). For example, pinnipeds relying on a protein-rich diet need to consume more prey mass to match the caloric value contained in a lipid-rich diet. Elevated dietary protein intake can then result in enhanced rates of protein catabolism, excretion of ^{14}N, and enrichment of ^{15}N in tissues (Zhao et al. 2006b). The amount of carbon and nitrogen assimilated from each prey source was not incorporated into the mixing model. This information is not available for ice seals and is beyond the scope of this study. In addition, prey items were combined into trophic guilds and adding elemental concentration values is inappropriate as the digestive efficiencies and assimilation rates of seals may differ for each assorted prey item within the trophic guilds, e.g., chitinous exoskeleton of shrimp versus lipid-rich fish (Keiver et al. 1984; Lawson et al. 1997b; Trumble et al. 2003).

In conclusion, interannual differences in diet of highly migratory Arctic pinnipeds can be revealed by analysis with isotopic mixing models. Grouping of potential prey sources eliminates the ability to examine important contributing sources at high

taxonomic resolution. Combining prey sources, however, allows identification of ecologically important prey groups and documentation of changes over time. This study provides evidence that ice seals are able to alter their foraging habits and thus may adjust to changes in food-web structure, giving them some resiliency to the effects of climate change on trophic dynamics.

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TABLES

Table 2.1 Inventory of Stable Isotope Signatures from Ice Seals. Stable carbon and nitrogen isotope ratios for muscle of ice seals during each year. Number of samples analyzed in Bayesian isotopic mixing models (*n*) and parenthesis display the number of samples that were stored in ethanol.

Species	Year of Collection	*n*	$\delta^{13}C$ [‰] Non-Lipid-Extracted	$\delta^{15}N$ [‰] Non-Lipid-Extracted
Bearded Seal (*Erignathus barbatus*)	2003	58	-17.84 ± 0.66	17.05 ± 0.84
	2008	52 (5)	-17.65 ± 1.00	16.24 ± 0.90
	2009	60	-17.89 ± 1.29	16.60 ± 0.88
	2010	43	-17.85 ± 0.91	16.03 ± 0.81
Total (*n*)		**213**		
Spotted Seal (*Phoca largha*)	2003	29	-18.35 ± 0.63	17.99 ± 0.86
	2008	20	-18.33 ± 0.61	17.15 ± 0.78
	2009	56	-19.07 ± 0.85	17.64 ± 0.63
Total (*n*)		**105**		
Ringed Seal (*Pusa hispida*)	2003	31	-19.60 ± 1.61	16.84 ± 0.65
	2008	14 (5)	-18.73 ± 0.77	16.51 ± 0.64
	2009	14	-18.88 ± 1.07	16.46 ± 1.00
	2010	22	-18.93 ± 0.35	16.72 ± 0.73
Total (*n*)		**81**		
Total Sample Size (*n*)		**399**		

Table 2.2 Inventory of Stable Isotope Signatures from Prey of Ice Seals. Stable carbon and nitrogen isotope ratios for select fishes and invertebrate prey of ice seals. Number of samples analyzed in Bayesian isotopic mixing models (*n*). Shaded columns are values used in models. (N/A, not available)

Species	Tissue/ Mixing Model Grouping	Year of Collection	*n*	$\delta^{13}C$ [‰] Non-Lipid-Extracted	$\delta^{13}C$ [‰] Lipid-Extracted	$\delta^{15}N$ [‰] Non-Lipid-Extracted	$\delta^{15}N$ [‰] Lipid-Extracted	Source
Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*)	Whole Demersal Fishes	2009	10	-19.28 ± 0.60	-17.88 ± 0.55	15.53 ± 0.49	15.50 ± 0.98	this study
Bering Flounder (*Hippoglossoides robustus*)	Whole Demersal Fishes	2009	10	-19.67 ± 0.99	-18.36 ± 0.30	15.25 ± 0.68	15.38 ± 0.72	this study
Polar Eelpout (*Lycodes polaris*)	Whole Demersal Fishes	2009	10	-18.84 ± 0.56	-17.77 ± 0.75	15.44 ± 0.45	15.73 ± 0.70	this study
Shorthorn Sculpin (*Myoxocephalus scorpius*)	Whole Demersal Fishes	2009	10	-19.13 ± 0.42	-17.75 ± 0.78	14.96 ± 0.78	14.83 ± 1.26	this study
Slender Eelblenny (*Lumpenus fabricii*)	Whole Demersal Fishes	2009	10	-19.44 ± 0.40	-17.64 ± 0.57	15.09 ± 0.78	14.88 ± 1.05	this study
Stout Eelblenny (*Anisarchus medius*)	Whole Demersal Fishes	2009	10	-19.36 ± 0.76	-17.71 ± 0.69	16.00 ± 0.52	15.98 ± 0.79	this study
Arctic Cod (*Boreogadus saida*)	Whole Pelagic Fishes	2009	10	-21.17 ± 0.63	-19.50 ± 0.32	14.24 ± 0.69	14.96 ± 0.66	this study
Capelin (*Mallotus villosus*)	Whole Pelagic Fishes	2009	10	-21.90 ± 0.74	-19.63 ± 0.27	13.09 ± 0.53	13.85 ± 0.44	this study
Pacific Herring (*Clupea pallasii*)	Whole Pelagic Fishes	2009	10	-22.85 ± 0.57	-20.72 ± 0.59	14.07 ± 0.66	14.71 ± 0.41	this study
Pacific Sand Lance (*Ammodytes hexapterus*)	Whole Pelagic Fishes	2009	10	-22.11 ± 0.95	-19.53 ± 0.40	13.05 ± 1.02	13.77 ± 0.90	this study
Rainbow Smelt (*Osmerus mordax*)	Whole Pelagic Fishes	2009	10	-23.87 ± 0.27	-23.09 ± 0.35	13.53 ± 0.45	14.21 ± 0.51	this study
Saffron Cod (*Eleginus gracilis*)	Whole Pelagic Fishes	2009	10	-20.80 ± 0.84	-19.70 ± 1.08	13.42 ± 0.52	13.88 ± 0.27	this study
Spider Crab (*Hyas coarctatus*)	Decapod – Crab	2004	8	-18.48 ± 0.32	N/A	15.22 ± 0.82	N/A	Iken et al. 2010
Common Shrimp (*Crangon* spp.)	Decapod – Shrimp	2004	3	-17.35 ± 0.23	N/A	14.97 ± 0.56	N/A	Iken et al. 2010
Greenland Cockle (*Serripes groenlandicus*)	Bivalves and Polychaetes	2004	6	-17.74 ± 0.31	N/A	8.07 ± 1.05	N/A	Iken et al. 2010
Arctic Krill (*Thysanoessa rashii*)	Planktonic Crustacean	N/A	N/A	N/A	-19.69 ± 0.96	N/A	12.25 ± 1.16	Iken unpublished*

* Katrin Iken. University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, 227 O'Neill, P.O. Box 757220, Fairbanks, AK 99775-7220. Notification of unpublished data: November 2010.

Table 2.3 Isotopic Mixing Model Results for the Muscle of Ice Seals. Proportional contribution of selected prey items for ice seals by year. Data are provided as lower and upper 95% confidence intervals as determined by the SIAR mixing model. Demersal and pelagic fishes are comprised of several species (N/A, not applicable).

		Prey taxa						
Species	Year	Demersal Fishes	Pelagic Fishes	Smelt (*Osmerus mordax*)	Crab (*Hyas coarctatus*)	Shrimp (*Crangon* spp.)	Bivalve (*Serripes groenlandicus*)	Euphausiid (*Thysanoessa rashii*)
Bearded Seal								
(*Erignathus barbatus*)	2003	2.7–58%	0.0–35%	3.8–24%	5.7–66%	N/A	0.0–5.6%	N/A
	2008	6.9–52%	0.2–44%	0.1–17%	1.5–51%	N/A	5.0–17%	N/A
	2009	3.3–53%	0.4–45%	1.5–22%	1.6–55%	N/A	0.0–9.1%	N/A
	2010	2.0–45%	0.0–51%	2.0–24%	1.1–47%	N/A	5.0–17%	N/A
Spotted Seal								
(*Phoca largha*)	2003	12–62%	0.0–27%	22–39%	N/A	0.0–38%	N/A	0.0–12%
	2008	9.0–60%	0.0–27%	23–44%	N/A	0.0–39%	N/A	0.0–11%
	2009	31–56%	0.0–9.0%	40–50%	N/A	0.0–17%	N/A	0.0–3.7%
Ringed seal								
(*Pusa hispida*)	2003	34–55%	0.0–19%	33–58%	N/A	N/A	N/A	0.0–7.8%
	2008	22–50%	0.0–47%	14–41%	N/A	N/A	N/A	0.0–27%
	2009	14–48%	0.0–47%	13–44%	N/A	N/A	N/A	0.0–33%
	2010	31–54%	0.0–27%	34–51%	N/A	N/A	N/A	0.0–10%

FIGURES

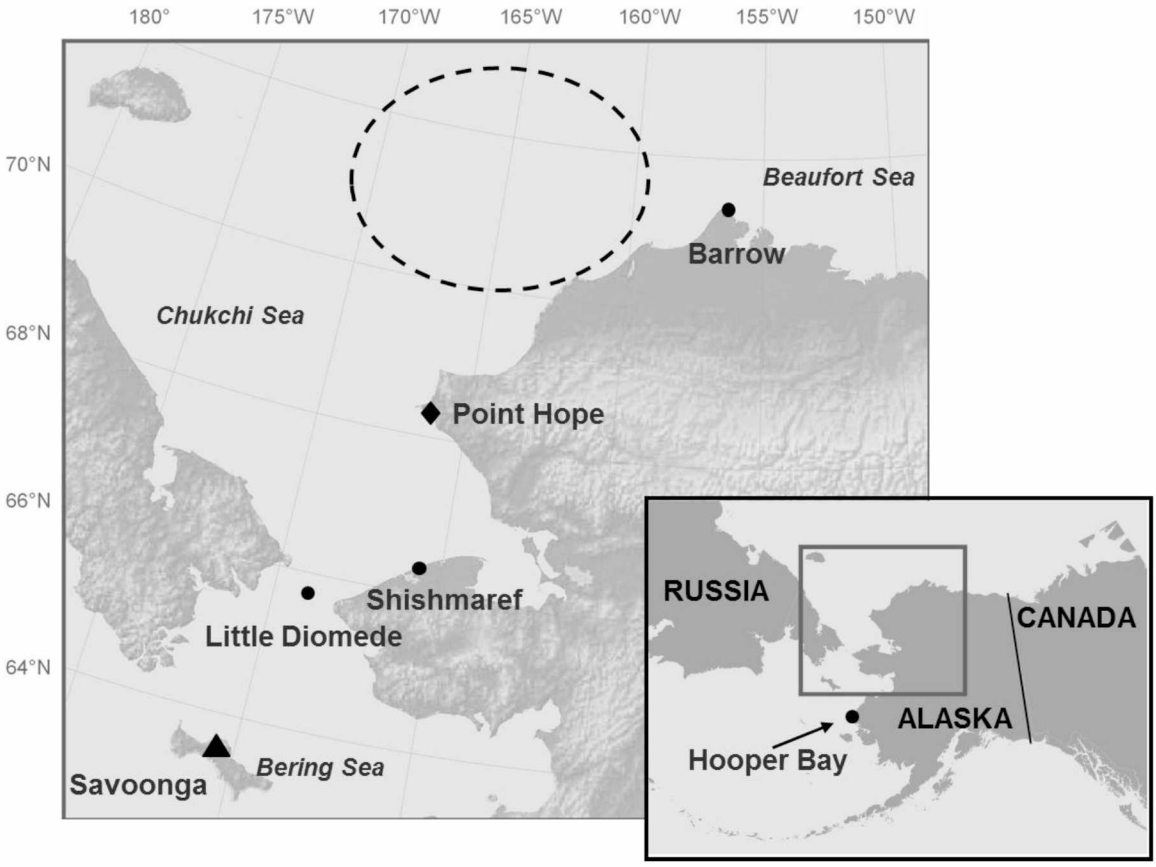

Figure 2.1 Sample Collection Map. Location map showing Alaska Native subsistence communities where ice seal samples were collected. Dashed circle indicates region where fishes were caught. Solid symbols indicate subsistence communities where seals were harvested in 2003 and 2008–2010 (circle), 2003 only (triangle), and 2008–2010 only (diamond).

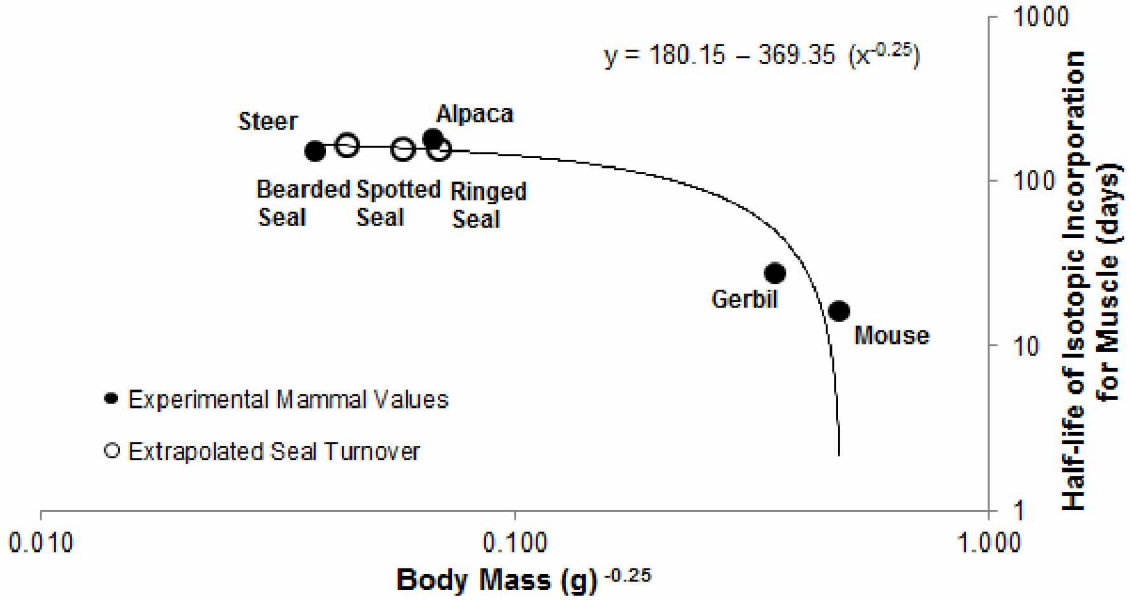

Figure 2.2 Muscle Turnover Based on Body Mass. Half-life of stable isotope integration into tissue (muscle turnover in days) based on an average total body mass in grams, i.e., half-life of carbon turnover = mass$^{-0.25}$ (Carleton and Martínez del Rio 2005). Experimental results for terrestrial mammals (solid circles, Tieszen et al. 1983; MacAvoy et al. 2005; Sponheimer et al. 2006; Bahar et al. 2009) were used to create a curvilinear regression; y = 180.15 – 369.35 ($x^{-0.25}$). This regression equation was then used to estimate muscle turnover for ice seals (open circles).

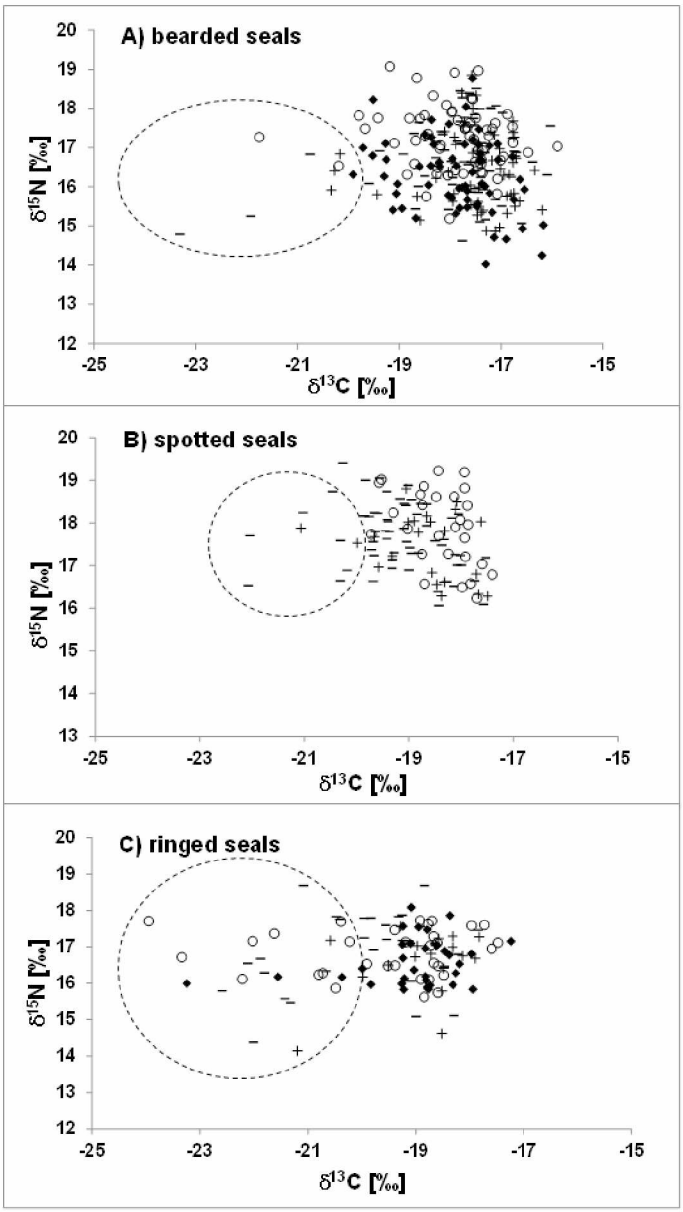

Figure 2.3 Stable Isotope Signatures for Sampled Population of Ice Seals. Stable carbon and nitrogen isotope ratios for muscle of A) bearded, B) spotted, and C) ringed seals. Symbols represent harvest year for individual seals, i.e., 2003 (open circle), 2008 (cross), 2009 (line), and 2010 (solid diamond). Dashed circle shows individuals likely feeding on smelt.

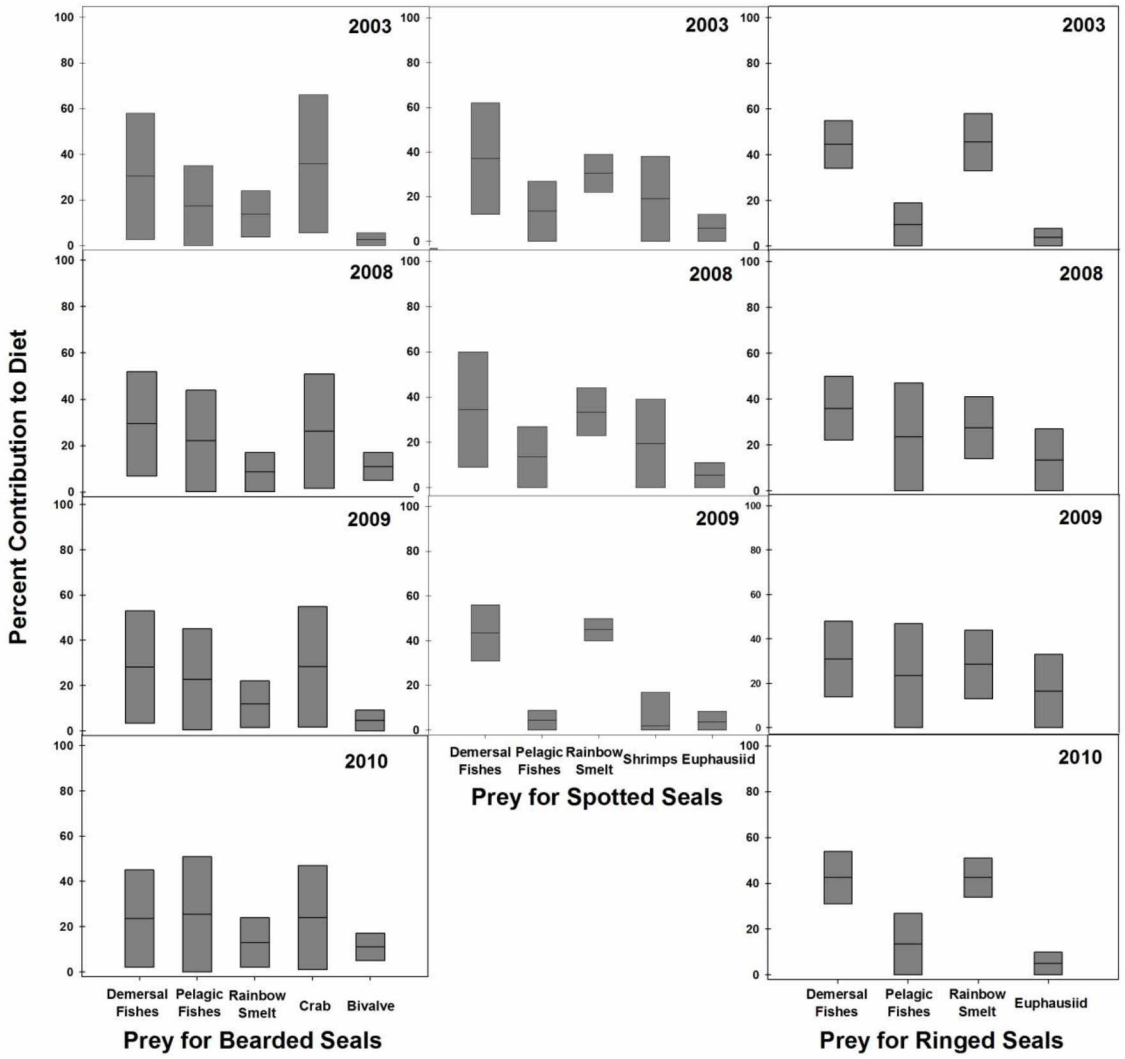

Figure 2.4 Isotopic Mixing Model Results for the Muscle of Ice Seals. SIAR mixing model results (based on muscle) of estimated proportion of prey sources in the diet of bearded, spotted, and ringed seals harvested for subsistence use in 2003, 2008–2010. Results are presented as mean (black line) and 95% confidence intervals (gray bars). Some prey items are combined in trophic guilds and are comprised of several species.

CHAPTER 3:

Diet History of Ice Seals Using Stable Isotope Ratios in Claw Growth Bands[3]

ABSTRACT

Climate change and sea ice reduction may lead to modifications of food-web structure in the Arctic, and this may impact foraging of ice-associated predators. We examined the dietary history recorded in claws of ringed (*Pusa hispida*), bearded (*Erignathus barbatus*), spotted (*Phoca largha*), and ribbon seals (*Histriophoca fasciata*) to describe potential interannual changes in their foraging. Seasonal keratin layers deposited in claws can document trophic history up to about 10 years. A total of 61 claws were collected during Alaska Native subsistence harvests in 2007–2010 and seasonal growth bands were examined for stable nitrogen and carbon isotope ratios to assess long-term diet patterns. Growth bands in claws from spotted seal pups were enriched in ^{15}N and depleted in ^{13}C suggesting maternal nutrient transfer. Ontogenetic shifts in trophic position were observed for spotted and ribbon seals. During 2007 (record ice minimum), proportionally more ringed seals fed at a lower trophic level, while spotted seal adults and young-of-the-year fed at a lower trophic level during 2006. Bearded seals may have been foraging more pelagically from 2008 to 2010. Interannual variations and high variability among species and individual diets illustrate the opportunistic nature and flexibility of ice seals to changes in prey.

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[3] Carroll, S.S., Horstmann-Dehn, L., and Norcross, B.L. 2012. Diet history of ice seals using stable isotope ratios in claw growth bands. Prepared for submission to the Canadian Journal of Zoology.

INTRODUCTION

In the last decade, Arctic sea ice has decreased in extent and thickness. Minimum sea ice extent occurs in September, and was lowest in 2007 relative to the average from satellite records during 1979–2000 (NSIDC 2011a). In the following summers since 2007, less of the thicker multi-year ice persisted leading to the second lowest ice extent on record in 2011 (NSIDC 2011a). In response to sea-ice habitat loss and predicted reduced snow cover, the National Oceanic and Atmospheric Administration (NOAA) has proposed to list the Arctic Basin population of ringed seals (*Pusa hispida*) and the Pacific population of bearded seals (*Erignathus barbatus*) as threatened under the Endangered Species Act (ESA; NOAA 2011a). A decision was made not to list the Bering Sea population of spotted seals (*Phoca largha*) in 2009 (NOAA 2009) or ribbon seals (*Histriophoca fasciata*) in 2008 (NOAA 2008) because sea ice in the Bering Sea is expected to persist in winter and is not present in summer and therefore not affected by the summer sea ice minima of the Arctic Ocean. Due to lawsuits, however, NOAA will be revisiting the status of ribbon seals in 2012 (NOAA 2011b).

Ice seals may be directly impacted by climate change as the sea ice platform they use for resting, pupping, and molting diminishes, along with more subtle indirect effects on prey resources. Changes in sea ice will likely lead to changes in the distribution and abundance of prey resources (Grebmeier et al. 2006; Grebmeier 2012). Consequently, the loss of sea ice may decrease benthic prey for bearded seals (Grebmeier et al. 2006; Bluhm and Gradinger 2008) resulting in decreased body condition. Lower body condition of female ringed seals has been correlated to lower ovulation rates in Canada, and years

of low ice can cause additional negative impacts on fecundity (Harwood et al. 2000). Moreover, nutritional stress can hinder the immune response of marine mammals and increase susceptibility to disease (Burek et al. 2008). In December 2011, NOAA declared an unusual mortality event for ringed seals and other ice-associated pinnipeds in the Arctic characterized by delayed or unusual molt, skin lesions, internal organ lesions, and immune system changes (NOAA 2011c). The cause of the outbreak has not been found. Overall, examining the feeding ecology of ice seals may give insight into the well-being of the species population.

The four species of ice seals in Alaska use different habitats within the Arctic ecosystem (Simpkins et al. 2003) and have diverse feeding ecologies. Ringed seals prefer land-fast ice along the coast and have a diet predominantly comprised of ice-associated prey, i.e., gadids, euphausiids, amphipods, and mysids (McLaren 1958; Lowry et al. 1980a; Quakenbush et al. 2010a). In contrast, bearded seals are typically benthic foragers and are found in drifting pack ice over shallow coastal areas (Burns and Frost 1979; Lowry et al. 1980b; Dehn et al. 2007). Common prey items found in the stomachs of bearded seals are demersal fishes, e.g., eelpouts, flatfishes, pricklebacks, and sculpins, as well as benthic invertebrates, e.g., bivalves, crabs, and shrimps (Johnson et al. 1966; Finley and Evans 1983; Quakenbush et al. 2010b). However, bearded seals also may consume pelagic fish species, such as capelin (*Mallotus villosus*) (Antonelis et al. 1994). Spotted seals are found in broken ice floes near the ice front during the winter/spring and during the open water season they make frequent visits to coastal haulouts (Lowry et al. 1998). Spotted seals feed on similar fish and invertebrate species as both ringed and

bearded seals (Gol'tsev 1971; Bukhtiyarov et al. 1984; Quakenbush et al. 2009). Ribbon seals are associated with loose pack ice during the breeding season and then become pelagic when waters are ice free (Burns 1970). Less is known about the diet of ribbon seals compared to the other seal species, but prey items include demersal and pelagic fishes, amphipods, bivalves, cephalopods, crabs, euphausiids, and decapod shrimps (Shustov 1965; Frost and Lowry 1980).

While the four species of ice seals feed on similar prey taxa, the proportions of prey consumed differs creating distinct stable isotope signatures for each species (Chapter 2). Stable nitrogen and carbon isotope ratios have been used extensively to study food-web structure in the Arctic (Hobson and Welch 1992; Bentzen et al. 2007; Dehn et al. 2007; Iken et al. 2010). Stable nitrogen isotope ratios describe the trophic level at which an individual feeds with stepwise enrichment of ^{15}N occurring from low to higher trophic levels (Peterson and Fry 1987; Kelly 2000). Carbon isotope ratios have been used to determine carbon source and illustrate habitat use (Schell et al. 1989; Dehn et al. 2007). For example, benthic organisms rely on organic material from surface waters that ultimately undergoes bacterial remineralization, leading to tissues enriched in ^{13}C compared to pelagic organisms that consume fresh phytoplankton (McConnaughey and McRoy 1979). Thus, predators consuming benthic prey items have tissues more enriched in ^{13}C than those feeding pelagically (e.g., Dehn et al. 2007). Compared to feeding ecology studies using stomach contents to document ingested prey, stable isotopes have the distinct advantage in that samples can be obtained minimally invasively, and they can

elucidate dietary nitrogen and carbon that has been assimilated and integrated into tissues over a period of time depending on the tissue examined.

Long-term dietary records can be recorded in continuously growing, metabolically inert keratin and dentine structures (Schell et al. 1989; Cherel et al. 2009; Newsome et al. 2009). Stable nitrogen and carbon isotope ratios of ringed seal claws have been analyzed to provide a long-term feeding record (Ferreira et al. 2011) and seasonal growth bands in seal claws are used to estimate minimum age, up to 10 years (McLaren 1958; Burns 1967; Benjaminsen 1973). Ringed and bearded seals use their claws to maintain breathing holes (Smith and Stirling 1975) resulting in wear at the tip of the claw, i.e., oldest growth. The exact timing in the deposition of alternating light and dark growth bands is uncertain, but it is generally accepted that the light band represents summer growth and the dark band winter growth (McLaren 1958; Benjaminsen 1973). Each set of light and dark bands represents a year of growth for the seal (Benjaminsen 1973). Stable nitrogen and carbon isotope ratios of growth layer groups in ringed seal claws illustrated interannual variation in diet among individuals (Ferreira et al. 2011). The overall goal of this study was to examine stable nitrogen and carbon isotope ratios in seasonal growth bands of ringed, bearded, spotted, and ribbon seal claws to infer feeding strategy. Specific objectives included: 1) describe general diet history for each species over the time period recorded in claws, 2) examine species-specific feeding history among the sampled population for interannual differences, particularly during the minimum sea ice extent of 2007, 3) examine potential age related differences in foraging

strategy, and 4) examine fetal, nursing, and post weaning stable isotope signatures in claws when possible.

MATERIALS AND METHODS

Claws of ringed, bearded, spotted, and ribbon seals were collected during Alaska Native subsistence harvests in the coastal communities of Barrow, Point Hope, Shishmaref, Little Diomede, and Hooper Bay (Figure 3.1). Ringed seal sampling occurred during late winter through fall of 2008–2010. Bearded seals were collected during summer 2008–2010, during fall of 2009 for spotted seals, and summer 2007 and winter 2010 for ribbon seals. The whole front flipper or a single front-flipper claw was collected shortly after death (less than 12 hours), stored in Ziploc® or Whirlpak™ bags, and frozen at –20 °C. Ice seals were obtained under the authority of National Marine Fisheries Service Scientific Research Permit Numbers 358-1585 and 358-1787 issued to the Alaska Department of Fish and Game, Arctic Marine Mammal Program (ADFG-AMMP) and DWM-814-1899 issued to the North Slope Borough, Department of Wildlife Management.

Fifty-six claws from all species of various ages (Table 3.1) were prepared. The distal phalanx was cut from the front flipper and claws were trimmed of fur and tissue. Each claw was labeled with a unique identifier and placed in a glass vial filled with distilled water and situated in a water bath. Claws were soaked in an ultrasonic water bath (Branson 3510, frequency of 40 kHz) at 38 °C for a minimum of 30 min or until the ungual crest at the base of the claw softened. The ungual crest and remaining cuticle skin were carefully shaved off with a scalpel blade. Each claw was placed back into a glass

vial with a 2:1 chloroform:methanol solution completely covering the claw. Vials were returned to the water bath and agitated for 10 min at 38 °C. Even though keratin is mostly free of lipids, the chloroform:methanol mixture was used to remove residual deposits from the claw surface. Solvent was replaced with distilled water and each claw sonicated for an additional 10 min. After cleaning, claws were immersed in distilled water to enhance the visibility of the seasonal bands and photographs and sketches were produced. The lateral surface of each seasonal band was drilled to a depth of less than 0.5 mm using a Dremel Stylus^{TM} Lithium-ion Cordless Rotary Tool (model: 1100-01) equipped with a size 105 engraving cutter to obtain keratin powder for stable nitrogen and carbon isotope analysis. Drilling speed was set to 10 000–14 000 rpm. Bands were drilled starting from the base to the tip of the claw, i.e., most recent to oldest growth. Light seasonal bands were drilled first followed by the dark seasonal bands. Seasonal bands matched findings by McLaren (1958) with light bands representing spring/summer growth, i.e., April–July, and dark bands displaying fall/winter growth, i.e., August–March (Table 3.1). For young seals (1–3 yr) additional sections were drilled to document potential pre-natal (formed during gestation) and constriction region/natal notch (formed around time of parturition; as described by McLaren 1958) stable isotope signatures (Figure 3.2). The pre-natal region was drilled about one centimeter from the tip of the claw. Keratin powder from each band was collected using weigh paper and stored in 1 mL glass vials. In addition to the 56 claws, all five claws from a front flipper of a single male ringed seal were drilled to compare claws within an individual for variability of stable isotope ratios (Table 3.1). All seal ages were estimated by counting growth layer groups in the cementum of canine

and postcanine teeth (Stewart et al. 1996), and these ages were verified against claw minimum age estimates (McLaren 1958). Age estimates ranged from 4 to 37 years for ringed, 5 to 20+ years for bearded, 1 to 8 years for spotted, and 8 to 13 years for ribbon seals (Table 3.1).

Samples from seasonal bands of claws were analyzed for $\delta^{15}N$ and $\delta^{13}C$ values at the Alaska Stable Isotope Facility at UAF. A subsample of claw powder, 0.2–0.4 mg, was weighed into tin capsules using a micro-balance (Sartorius Model MP2). $\delta^{15}N$ and $\delta^{13}C$ values were determined using a Finnigan MAT Delta^{Plus}XP Isotope Ratio Mass Spectrometer (IRMS) directly coupled to a Costech Elemental Analyzer (ESC 4010). Stable isotope ratios are expressed in conventional delta (δ) notation:

[1] $$\delta X\,(‰) = ((R_{sample}/ R_{standard}) - 1) \times 1\,000$$

where X is ^{15}N or ^{13}C and represents the relative difference between isotope ratios of the sample (R_{sample}, $^{15}N/^{14}N$ or $^{13}C/^{12}C$) and standard gases, i.e., atmospheric N_2 and Vienna Pee Dee Belemnite, respectively. Peptone was used as a laboratory-working standard and was run every 10 samples. The precision of analysis, expressed as one standard deviation from multiple analyses of peptone (n = 106) conducted during the runs of samples for $\delta^{15}N$ and $\delta^{13}C$, was 0.1‰ and < 0.1‰, respectively.

Prior to data analysis, all seal claw samples were corrected for the Suess Effect. Fossil fuels are depleted in ^{13}C (Keeling 1979). As the amount of anthropogenic CO_2 released into the atmosphere increases, a higher amount of dissolved organic carbon depleted in ^{13}C is exchanged from the atmosphere to the ocean, i.e., Oceanic Suess Effect

(Revelle and Suess 1957). The following Suess Effect correction factor was used by Misarti et al. (2010) for Arctic marine mammals:

[2] $$\text{Suess Effect Correction Factor} = a^{(b*0.027)}$$

This correction factor was applied to the $\delta^{13}C$ value of each seasonal band in accordance with the year represented by the band. The variable *a* represents the maximum annual rate of $\delta^{13}C$ decrease in the North Pacific (i.e., –0.014, Quay et al. 1992) and variable *b* corresponds to the year of claw band deposition minus 1850, i.e., the start of the Industrial Revolution. An additional correction was proposed by Misarti et al. (2010) to account for the discrimination by primary producers for ^{13}C in response to elevated CO_{2aq} in the ocean as CO_{2atm} increases. However, this factor was not applied to data in this study because it is a small correction similar to instrument error and parameters needed for this calculation, i.e., cell growth rate, surface area of the cell, salinity, and sea surface temperatures, are variable across ice seal geographic range (within and among species) and thus make it difficult to generalize.

Statistical analyses were performed in R (Version 2.11.1, R Development Core Team 2011) and a *p*-value less than 0.05 was considered significant. For spotted seal pups, a mean value and standard deviation for the change in isotope ratios during each developmental stage, e.g., gestation to parturition, was calculated. $\delta^{15}N$ and $\delta^{13}C$ values corresponding to the period of gestation, parturition, and nursing were removed from the analysis of juveniles and adults seals to examine feeding history of individuals excluding the possible bias related to maternal nutrient transfer. A Pearson's correlation test was

applied to examine variability among claws from the same individual. A mixed-effects model with temporal pseudoreplication was run independently for each species in R for both $\delta^{15}N$ and $\delta^{13}C$ values of ringed, bearded, and spotted seal claws. The standard deviation of $\delta^{15}N$ and $\delta^{13}C$ values across seal individuals within a species was extracted from the mixed-effects model and used to calculate a standard error for each season. Two standard errors from the species mean isotope value were used to create confidence intervals for both $\delta^{15}N$ and $\delta^{13}C$ values of each species. Studentized residuals greater than two were considered outliers. In general, confidence intervals represent typical stable isotope values for each species and studentized residuals depict unusual values or "anomalies". Moreover, standard deviations from the mixed-effects model were used to calculate the percent contribution of variability from each source, i.e., among individual seals, season, and residual error. To identify possible trends for interannual variations over the recorded diet history of ringed, bearded, and spotted seals, residuals for both $\delta^{15}N$ and $\delta^{13}C$ values of seasonal bands within an individual were normalized to the mean isotope value. These standardized residuals were compared across individuals within each species. Stable isotope graphs were created using SigmaPlot (SigmaPlot v.12.0).

RESULTS

Variation Among Digits

The $\delta^{15}N$ and $\delta^{13}C$ values of growth bands for each season across each claw (digit I–V) from the same individual were highly correlated (Table 3.2, Figure 3.3). When comparing growth bands from digit I–V, there was one fewer seasonal band present at the

tip of each consecutive claw, with approximately two years (4 seasonal growth bands) lost at the distal end of digit V (Figure 3.3).

Isotopic History by Species

Ringed Seal

Isotopic signatures for ringed seal claws were highly variable both seasonally and interannually within individuals, and no consistent seasonal pattern was apparent (Figure 3.4a, b, 3.5a, b). The range of $\delta^{15}N$ values in growth bands of ringed seal claws among individuals was 14.0 to 19.4‰, with maximum variations in seasonal bands within individuals ranging from 0.4‰ and 2.4‰ (Figure 3.4a). Typical $\delta^{15}N$ values ranged from 16.8 to 17.4‰, based on confidence intervals over the time period of the largest sample size (i.e., fall/winter 2001 to spring/summer 2009; $n > 10$ seals). $\delta^{13}C$ values in seasonal bands of ringed seal claws among individuals ranged from −21.1to −14.6 ‰, with maximum variations in seasonal bands within individuals ranging from 0.5‰ and 1.5‰, excluding one individual having a variation of 5.4‰. Large seasonal fluctuations in $\delta^{13}C$ were observed for this one ringed seal with $\delta^{13}C$ values decreasing by more than 3.5‰ below the lower confidence interval during fall/winter 2001 and 2003 (Figure 3.5a). Typical $\delta^{13}C$ values ranged from −17.0 to −16.0‰, based on confidence intervals over the time period of the largest sample size (i.e., fall/winter 2001 to spring/summer 2009; $n > 10$ seals).

Bearded Seal

Isotopic variability was high among bearded seals (Figure 3.6a, b, 3.7a, b). $\delta^{15}N$ values in seasonal growth bands of bearded seal claws among individuals ranged from

14.6 to 18.2‰, with maximum variations in seasonal bands within individuals ranging from 0.5‰ and 1.2‰ (Figure 3.6a). Typical $\delta^{15}N$ values ranged from 16.3 to 16.9‰, based on confidence intervals over the time period of the largest sample size (i.e., fall/winter 2003 to spring/summer 2008; $n > 10$ seals). Variability of $\delta^{13}C$ values among individual bearded seals was also high; however, $\delta^{13}C$ values were relatively stable within each individual (Figure 3.7a). $\delta^{13}C$ values in seasonal growth bands of bearded seal claws among individuals ranged from −18.3 to −13.7‰, with maximum variations in seasonal bands within individuals ranging from 0.2‰ and 1.7‰. Typical $\delta^{13}C$ values ranged from −16.3 to −15.4‰, based on confidence intervals over the time period of the largest sample size (i.e., fall/winter 2003 to spring/summer 2008; $n > 10$ seals).

Spotted Seal

Our sample of claws for spotted seals included young animals (1–3 yr) and allowed us to examine the isotopic differences among fetal, natal, nursing, and post weaning time periods. For spotted seal pups, $\delta^{15}N$ values increased and $\delta^{13}C$ values generally decreased from gestation to nursing (Figure 3.8a). $\delta^{15}N$ values increased by 1.2 ± 0.5‰ from gestation to parturition (mean change in stable isotope ratios ± SD) for 79% of claws for all spotted seals. The remaining claw bands representing this period showed an increase in $\delta^{15}N$ values by < 0.5‰. The pattern for $\delta^{15}N$ between parturition and nursing was not consistent as $\delta^{15}N$ values for some claws increased while others decreased. $\delta^{13}C$ decreased by 0.9 ± 0.6‰ from gestation to nursing for 79% of pups,

while $\delta^{13}C$ for the remaining 21% of pups increased by 0.6 ± 0.4‰ from gestation to nursing.

For spotted seal juveniles, stable nitrogen and carbon isotopic signatures after nursing were generally constant with the exception of four seals. $\delta^{15}N$ values decreased by 1.3 ± 0.5‰ between nursing and first winter foraging (mean change in stable isotope ratios ± SD) in all spotted seal pups (Figure 3.8a). For four of 14 individuals, $\delta^{15}N$ values increased over the next four foraging seasons (Figure 3.8b). A general increase in $\delta^{15}N$ values, however, was not apparent for all juveniles after their first winter foraging as claws for these seals had higher $\delta^{15}N$ values compared to the four seals, i.e., values greater than 16‰ (Figure 3.8b). $\delta^{13}C$ values did not vary for the majority of juvenile seals during subsequent foraging seasons, and values ranged from −16.8 to −13.5‰ (Figure 3.8b).

Subadult and adult spotted seals (> 4 years) displayed high variability for $\delta^{15}N$ values among individuals, while $\delta^{13}C$ values were relatively stable (Figure 3.9a, b, 3.10a, b). $\delta^{15}N$ values in seasonal bands of spotted seal claws among individuals ranged from 15.3 to 17.7‰, with maximum variations in seasonal bands within individuals ranging from 0.5‰ and 1.3‰ (Figure 3.9a). Typical $\delta^{15}N$ values ranged from 16.3 to 17.3‰, based on confidence intervals over the time period of the largest sample size (i.e., fall/winter 2005 to spring/summer 2009; $n > 10$ seals). $\delta^{13}C$ values in spotted seal claws among individuals ranged from −16.7 to −14.8‰, with maximum variations in seasonal bands within individuals ranging from 0.3‰ and 1.1‰ (Figure 3.10a). Typical $\delta^{13}C$

values ranged from −15.7 to −15.2‰, based on confidence intervals over the time period of the largest sample size (i.e., fall/winter 2005 to spring/summer 2009; $n > 10$ seals).

Ribbon Seal

Ribbon seal claws showed a broad range of $\delta^{15}N$ values, but $\delta^{13}C$ values were similar across individuals and remained relatively stable over years (Figure 3.11a, 3.11b). Among individuals, $\delta^{15}N$ variability was high with one seal having lower values compared to the other two seals, i.e., minimum $\delta^{15}N$ value of 13.5‰ versus 17.8‰ for the other two seals (Figure 3.11a). Maximum variations in seasonal bands per individual ranged from 0.7‰ and 1.7‰. Generally, $\delta^{15}N$ values increased with seal age. $\delta^{13}C$ ranges for ribbon seal claw growth bands were similar to those of adult spotted seals, i.e., −17.1 to −14.9‰. Maximum variations in seasonal bands per individual ranged from 0.4‰ and 1.1‰.

Interannual Comparison

Proportionally more ringed seal claws of the sampled population showed a decrease in $\delta^{15}N$ values during 2007, while across all individuals $\delta^{13}C$ values decreased over time (Figure 3.4b, 3.5b). $\delta^{15}N$ values for 71% (12 of 17) of ringed seals decreased by 1.0 ± 0.3‰ from fall/winter 2006 to spring/summer 2008 (mean change in stable isotope ratios ± SD), with 58% (7 of 12) of the claws falling below the lower confidence interval (Figure 3.4a). Furthermore, $\delta^{15}N$ values for 50% (5 of 10) of ringed seal claws increased by 1.2 ± 0.4‰ from spring/summer 2008 to spring/summer 2010, while two seals did not have data beyond 2008 as they were harvested in 2008. Standardized

residuals displayed an overall decrease in $\delta^{15}N$ values during 2007 followed by a subsequent increase after 2008 (Figure 3.4b). An interannual trend for $\delta^{13}C$ values was not apparent when assessing claw isotope values (Figure 3.5a); however, standardized residuals revealed $\delta^{13}C$ values decreasing from 1998 to 2010 (Figure 3.5b).

During 2007, some bearded seal claws had lower $\delta^{15}N$ values compared to the previous years, whereas a decreasing trend in $\delta^{13}C$ values occurred after 2007. More specifically, $\delta^{15}N$ values for 56% (9 of 16) of bearded seals decreased by 1.0 ± 0.3‰ from fall/winter 2006 to spring/summer 2008 (Figure 3.6a). The remaining 44% (7 of 16) showed only minor deviations in $\delta^{15}N$ (< 0.5‰). Standardized residuals showed a decrease in $\delta^{15}N$ values from 1999 to 2000 and from 2006 to 2008 (Figure 3.6b); however, sample size was small during the earlier years, i.e., $n = 6$ seals. An interannual trend for $\delta^{13}C$ values was not apparent when assessing claw isotope values (Figure 3.7a); however, standardized residuals displayed lower $\delta^{13}C$ values from spring/summer 2008 to spring/summer 2010 compared to previous years (Figure 3.7b). Although, sample size was small after spring/summer 2008 (Figure 3.7a).

During 2006, $\delta^{15}N$ values were lower for young-of-the-year and adult spotted seals. Spotted seal pups generally had $\delta^{15}N$ values ranging from 18.5 to 19.5‰; however, during 2006, 71% (5/7) of nursing pups had lower $\delta^{15}N$ values ranging from 16.1 to 17.2‰ (Figure 3.8a). During fall/winter 2006, the two oldest seals, i.e., age 6+, showed a decrease in $\delta^{15}N$ values by about 0.8‰ (Figure 3.9a), dropping below the lower confidence interval. Standardized residuals displayed low $\delta^{15}N$ values during fall/winter

2006 for subadult/adult spotted seals; however, this was not lower compared to other years examined (Figure 3.9b). An interannual trend was not apparent for $\delta^{13}C$ values of subadult/adult spotted seal claws (Figure 3.10a) or when examining standardized residuals (Figure 3.10b). Overall, variations in $\delta^{15}N$ or $\delta^{13}C$ values were high among individuals for ringed, bearded, and spotted seals, while time period contributed less to the total variance (Table 3.3).

DISCUSSION

Similar isotopic signatures were obtained from growth bands regardless of which digit the claw came from (Table 3.2, Figure 3.3). However, fewer growth bands were retained on the shorter digits, i.e., digits III–V (Figure 3.3). Thus, digit I or II should be collected and analyzed for the longest possible diet history. In addition to the low variation between digits, the high correlation among digits in this study also confirms the consistency of our methods and our ability to obtain keratin powder from specific growth bands. A significant correlation among ringed seal digits was also documented by Ferreira et al. (2011) and they also recommended digit I or II because they are larger in size and have clear growth bands.

The relatively depleted isotopic signatures of ringed seal claws compared to bearded seal claws are consistent with a primarily pelagic feeding strategy (Kovacs 2007), but may also indicate feeding in the Beaufort Sea, a region known to be depleted in ^{13}C (Saupe et al. 1989; Schell et al. 1989; Dunton et al. 2006). Ringed seals may consume a mixture of pelagic crustaceans and fishes, but prey proportions are highly variable by season and region (Lowry et al. 1980a). The range in $\delta^{15}N$ values spans about

two trophic levels within the sampled ringed seal population, i.e., 3‰ per trophic level (Peterson and Fry 1987), but also vary widely within individuals. The range and variability of $\delta^{15}N$ values agrees with a flexible and opportunistic diet of lower and higher trophic level prey. From late fall to early spring, ringed seal diet mainly consists of gadids and during summer invertebrates become more important (Johnson et al. 1966; Lowry et al. 1980a; Smith 1987). However, the results of our study indicate that a consistent seasonal switch in prey of different trophic levels, i.e., fishes versus krill, does not occur. On the other hand, epi-benthic shrimps (e.g., *Sclerocrangon* spp.) can be important prey for ringed seals during spring and summer (Lowry et al. 1980a) and have $\delta^{15}N$ values similar to demersal fishes (Iken et al. 2010). Thus, differences between summer and winter prey may not be detected based on $\delta^{15}N$ values depending upon the prey eaten even though a seasonal prey switch may have occurred. On average, $\delta^{15}N$ values were higher for all growth bands analyzed in this study compared to growth bands from ringed seals analyzed by Ferreira et al. (2011), i.e., 17.1 ± 0.8‰ compared to 15.6 ± 1.5‰ (mean ± SD), respectively. Higher $\delta^{15}N$ values observed in this study may be a result of a greater consumption of demersal fishes, e.g., sculpins (Cottidae) or pricklebacks (Stichaeidae), and epi-benthic shrimps by ringed seals in the Alaskan Arctic (Lowry et al. 1980a; Quakenbush et al. 2010a) than for the ringed seals in the Hudson Bay analyzed by Ferreira et al. (2011). In addition, lower $\delta^{15}N$ values in muscle from ringed seals in the Hudson Bay region were attributed to regional differences in food-web structure, i.e., shorter food chain, compared to seal muscle from other Arctic regions (Young et al. 2010). Typical $\delta^{13}C$ values for ringed seal claws were lower compared to

bearded seals, which may support pelagic foraging regardless of season for ringed seals, while bearded seals feed on benthic organisms more enriched in ^{13}C compared to pelagic organisms (Iken et al. 2010). The unusually depleted ^{13}C growth bands observed during fall/winter of 2001 and 2003, corresponding to the second and fourth fall/winter foraging for one ringed seal individual (Figure 3.5a), could be the result of consuming fairly depleted ^{13}C prey sources during these seasons, e.g., smelt (*Osmerus mordax*) or herring (*Clupea pallasii*). However, it is more likely that the depleted carbon signatures of this seal are due to foraging in the Beaufort Sea versus Chukchi Sea. Following a similar pattern, ice seal prey, i.e., cod, amphipod, and shrimp, from the Bering and Chukchi Seas are more enriched in ^{13}C compared to those from the eastern Beaufort Sea (Dunton et al. 1989, Saupe et al. 1989). Thus, unusually depleted signature for fall/winter growth bands of this ringed seal would be consistent with a Beaufort Sea signature. Correspondingly, Dehn et al. (2007) found differences in carbon isotope signatures in muscle of ringed seals harvested in Barrow (Chukchi/Beaufort Seas) versus Ulukhaktok, Canada (Beaufort Sea). Changes in feeding location between the Beaufort and Chukchi Seas have also been be illustrated as $\delta^{13}C$ oscillations in continuously growing baleen plates of bowhead whales (*Balaena mysticetus*) (Schell et al. 1989). Ringed seals in the Alaskan and Canadian Arctic are known to exhibit extensive movement ranges occupying the Bering, Chukchi, and Beaufort Seas (Crawford et al. 2011; Paulatuk Holman and Tyktoyaktuk Hunters and Trappers Committees 2011). On average, all growth bands from this study were more enriched in ^{13}C (-16.6 ± 0.9‰) relative to growth bands from ringed seals analyzed in Ferreira et al. (2011), i.e., -18.6 ± 0.8‰, -18.4 ± 0.7‰, and -17.1 ± 0.6‰ for

different areas within Hudson Bay. Similarly, muscle from seals harvested in the Hudson Bay were depleted in ^{13}C compared to seals from other Arctic regions and it was suggested that the depleted ^{13}C signatures were a result of terrigeneous input into the Hudson Bay (Young et al. 2010). Overall, high variability in $\delta^{15}N$ and $\delta^{13}C$ values among individuals from this study and Ferreira et al. (2011) illustrate the highly opportunistic nature of ringed seals.

Isotopic signatures of bearded seal claws are consistent with their benthic diet (Antonelis et al. 1994; Dehn et al. 2007; Quakenbush et al. 2010b) but there is high variability in diet among individuals. Bearded seals consume a variety of benthic and epi-benthic invertebrates, along with demersal and pelagic fishes (Kosygin 1971; Dehn et al. 2007; Quakenbush et al. 2010b). Isotope values for benthic prey are typically enriched in ^{15}N compared to pelagic food webs (Iken et al. 2005). However, typical $\delta^{15}N$ values for bearded seal claws were lower compared to ringed seals suggesting a high contribution of lower trophic level prey to the diets of bearded seals. Clams can be frequent prey for older bearded seals (Lowry et al. 1980b; Dehn et al. 2007; Quakenbush et al. 2010b), and this prey taxon is relatively depleted in ^{15}N compared to benthic scavengers (Iken et al. 2010). Muscle of bearded seals is enriched in ^{15}N compared to ringed seals (Young et al. 2010) or $\delta^{15}N$ is within similar ranges for both species (Dehn et al. 2007). Ultimately, $\delta^{15}N$ ranges can overlap between ringed and bearded seals as ringed seals may also feed on epi-benthic shrimps and demersal fishes (Quakenbush et al. 2010a) and bearded seals have a diverse diet of lower and higher trophic invertebrates, along with demersal and pelagic fishes (Quakenbush et al. 2010b). High variability in $\delta^{13}C$ values among

individual bearded seal claws in this study indicates diverse individual foraging strategies potential relating to individual prey preference and/or prey preferences among ages and between sexes. Smaller ranges in $\delta^{13}C$ have been documented for muscle among bearded seals (Hobson et al. 2002; Dehn et al. 2007). This study documented minimal variation in $\delta^{13}C$ over time for an individual, while simultaneously showing large variability among individuals (Figure 3.7a). The highest $\delta^{13}C$ values likely belong to a more focused benthic consumer in the Bering Sea, i.e., feeding on a food source enriched in ^{13}C in a region enriched in ^{13}C (Dunton et al. 2006), and the lowest $\delta^{13}C$ values suggest a more pelagic forager. Low variability in $\delta^{13}C$ values for individual bearded seals over time could be related to a preference for certain prey guilds (Dehn et al. 2007), although the high variability in $\delta^{15}N$ values suggests this is not the case. Foraging in the same general region throughout the time period recorded in claws may be more likely. Bearded seals tend to make seasonal migrations; during fall/winter they reside near the ice edge in the Bering Sea and as ice recedes they move to the southern edge of the Chukchi and Beaufort Seas pack ice for the duration of the summer (reviewed in Cameron et al. 2010; Boveng et al. 2012). While shifts in $\delta^{13}C$ values corresponding to season were not observed for bearded seals, they may have been masked by changes within prey, such as, seasonal changes in lipid content or regional differences in $\delta^{13}C$ values of prey. In fall/winter, shrimps and crabs are prevalent in bearded seal stomachs, while clams and fish occur more frequently during spring/summer (Johnson et al. 1966; Lowry et al. 1980b). Bearded seals may have been feeding on benthic organisms relatively enriched in ^{13}C, but in an area depleted in ^{13}C. For example, if bearded seals fed on benthic prey in

the Beaufort Sea, then switched to pelagic prey relatively depleted in ^{13}C, but from an area enriched in ^{13}C such as in the Bering Sea (Dunton et al. 2006) similar results could occur.

Stable isotope ratios in claws corresponding to pre- and post-natal growth in spotted seals provide information on nutrient transfer from the mother and its incorporation by the pup. All claws that included pre-natal growth bands showed an increase in $\delta^{15}N$ values from gestation to parturition consistent with transfer and fractionation of maternal protein to fetal development. This isotopic enrichment has been reported in both terrestrial and marine mammals using a variety of soft tissues and keratinized structures (Hobson et al. 2000; Jenkins et al. 2001; Stegall et al. 2008). The growth band immediately following the natal notch represents an integrated stable isotope signature of the spring/summer diet of the pup, which includes the nursing period. Spotted seal pups are born on ice floes between April and mid-May and begin foraging on their own in late May to early June (reviewed in Boveng et al. 2009). Thus, observed increase in $\delta^{15}N$ values from parturition to nursing corresponds to nursing and reliance on body reserves after weaning (Newsome et al. 2006). In contrast, observed decrease in $\delta^{15}N$ values from parturition to weaning likely reflects nursing combined with some feeding on lower trophic level prey. Spotted seal juveniles mainly consume crustaceans (e.g., gammarid amphipods; Gol'tsev 1971; Bukhtiyarov et al. 1984) but consumption of shrimps and pelagic fishes (e.g., sand lance, *Ammodytes hexapterus*; Arctic cod, *Boreogadus saida*; saffron cod, *Eleginus gracilis*) increase with seal age (Gol'tsev 1971; Bukhtiyarov et al. 1984). Foraging on higher trophic level prey, i.e., teleosts, varies with

individual juvenile seals (Burns 1999) and some claws from this study illustrated a gradual increase in trophic level foraging of seals, while others fed at a higher trophic level immediately after their first foraging season. Although, seasonal bands enriched in ^{15}N could result from a difficult transition to feeding after weaning where pups must rely on their own protein catabolism (Castellini and Rea 1992); however, it is unlikely to occur for more than two seasons and values were similar to nitrogen signatures of adult spotted seals. Phocid milk has a high fat content of about 40% (Oftedal et al. 1988; Iverson et al. 1993) so that seal pups quickly develop a blubber layer during a short nursing period. Milk with high lipid content is depleted in ^{13}C (Newsome et al. 2010) and this is reflected in continuous decrease in $\delta^{13}C$ values from gestation to the first claw growth band for seals in this study. In general, young-of-the-year have tissues enriched in ^{15}N and depleted in ^{13}C compared to their mothers (Polischuk et al. 2001) or other older individuals (Newsome et al. 2006; Dehn et al. 2007; Orr et al. 2011).

Spotted seal claws of subadults and adults showed high variability in trophic level foraging, but low variation in carbon source among individuals. Diets of spotted seals predominately consist of fishes, e.g., gadids, herring, walleye pollock (*Theragra chalcogramma*), sand lance, and smelt (Lowry et al. 1981; Bukhtiyarov et al. 1984; Dehn et al. 2007, Quakenbush et al. 2009). Other prey groups found in spotted seal stomachs include cephalopods, crustaceans, demersal fishes, and mollusks (Bukhtiyarov et al. 1984; Dehn et al. 2007; Quakenbush et al. 2009). A diet consisting mainly of fishes would have $\delta^{15}N$ values of about 17‰, i.e., Arctic cod are about 14.9 ± 0.6‰ (Iken et al. 2010) plus an enrichment factor of 2.3‰ for claws (Hobson et al. 1996). Therefore, $\delta^{15}N$

values show a diet mainly comprised of prey enriched in ^{15}N such as pelagic or demersal fishes, or epi-benthic shrimps. Growth bands depleted in ^{15}N occurred during the fall/winter season in spotted seals (Figure 3.9a) and this may be the result of consumption of ice-associated crustaceans, i.e., amphipods (Quakenbush et al. 2009). High variability in $\delta^{15}N$ values among individuals suggests a preference for certain prey types. For example, in this study a 4-year-old spotted seal fed trophically higher than older seals in this study. This may be the result of the younger seal foraging on decapod shrimps (Gol'tsev 1971; Bukhtiyarov et al. 1984), which can have higher $\delta^{15}N$ values similar to demersal fishes (Iken et al. 2010). $\delta^{15}N$ values of claws were on average about 1‰ lower for spotted seals than ringed seals (Figure 3.4a, 3.9a) in contrast to results from Dehn et al. (2007) where $\delta^{15}N$ values of muscle were 1‰ higher (reaching maximum values of about 19‰) for spotted seal than for ringed seals. Spotted seals in this study may have had a higher proportion of ice-associated crustaceans in their diet because younger seals dominated our sample (Table 3.1). Age related changes in the diet of spotted seals have been described previously, with young seals relying more on ice-associated crustaceans and the relative importance of fish increases with age (Gol'tsev 1971). Similarly, the upper range in $\delta^{15}N$ values for spotted seal muscle documented by Dehn et al. (2007) could be due to the incorporation of walleye pollock in seal diets. Walleye pollock can be enriched in ^{15}N compared to Arctic cod or herring as adult pollock feed on juvenile fishes (Kurle and Worthy 2001). The confidence interval for $\delta^{13}C$ values was similar in spotted and bearded seal claws with growth bands for these two species being relatively enriched in ^{13}C compared to ringed seals suggesting a mixed diet of benthic and pelagic prey, even

for juvenile and subadult spotted seals (Figure 3.8b). However, pelagic fishes occur more frequently in the diet of spotted seals compared to demersal fishes or benthic invertebrates, with the exception of decapod shrimps (Quakenbush et al. 2009). A diet high in pelagic (planktivorous) fish was also documented for spotted seals using fatty acid analysis (Cooper et al. 2009). Thus, it is more likely that growth bands enriched in ^{13}C are characteristic of foraging nearshore and under the sea ice. Nearshore habitats are enriched in ^{13}C relative to offshore regions; higher nutrient levels from upwelling leads to faster growth of primary producers, thus causing an enrichment of ^{13}C in these organisms (reviewed in Newsome et al. 2010). During the open-water season, spotted seals aggregate at coastal haulouts (reviewed in Boveng et al. 2009) near spawning areas of capelin and herring (Quakenbush 1988), where they rest between feeding bouts. Consumption of pelagic fishes that are foraging on prey sources nearshore would produce seal tissues enriched in ^{13}C. Although spotted seals are found nearshore in summer (enriched in 13C) and move offshore in winter (normally not enriched in ^{13}C) remaining close to the ice front in the Bering Sea (Burns 2002), the $\delta^{13}C$ values from their claws are similar between winter and summer. This suggests that spotted seals forage on ice-associated prey during the winter (enriched in ^{13}C). Spotted seals may be consuming Arctic cod underneath the sea ice and this fish species has a diet primarily consisting of copepods (*Calanus* spp.) and amphipods (*Gammarus wilkitzkii, Apherusa glacialis, Onisimus nanseni,* and *Onisimus glacialis*) (Lowry and Frost 1981; Bradstreet and Cross 1982; Lønne and Gulliksen 1989). Copepods (*Calanus* spp.) overwinter in deeper waters during a period of diapause (Gradinger 1995). However, amphipods (*G. wilkitzkii, A.*

glacialis, O. nanseni, O. glacialis) live permanently associated with the ice and feed mainly on detritus and some ice algae during the winter (Poltermann 2001). Both sources of carbon (detritus and ice algae) would produce consumer tissues enriched in ^{13}C (McConnaughey and McRoy 1979; Kennedy et al. 2002) leading to seal tissues enriched in ^{13}C.

Isotopic signatures of ribbon seal claws depict age-related differences in diet, high variation in trophic level foraging among individuals, and a stable carbon source. Juvenile and subadult ribbon seals have been found to consume lower trophic level crustaceans and then transition to foraging on fishes and cephalopods (Arsen'ev 1941; Fedoseev 2000; Dehn et al. 2007). In this study, a gradual increase in trophic level foraging was seen for two ribbon seals (Figure 3.11a). One ribbon seal had the lowest $\delta^{15}N$ values of any ice seal in this study and may have been diving deep in the Bering Sea (reviewed in Boveng et al. 2008) to consume squid as cephalopods can be depleted in ^{15}N (Kurle et al. 2011) compared to demersal fishes and decapods (Iken et al. 2010). Alternatively, this seal may have foraged on amphipods, euphausiids, and/or clams (Shustov 1965; Frost and Lowry 1980; Bukhtiyarov 1990), which would have a similar signature as squid. Demersal and pelagic fishes are primary prey for ribbon seals in spring (Shustov 1965; Frost and Lowry 1980; Bukhtiyarov 1990) consistent with spring/summer growth bands being more enriched in ^{15}N. However, the lack of seasonality in $\delta^{15}N$ values suggests that ribbon seals may also prey on higher trophic level, e.g., teleost prey, throughout the year. Ribbon seal $\delta^{13}C$ values were remarkably stable over the length of the claw with very little variation among individuals, season, and

years. This indicates that ribbon seals feed in areas with similar carbon sources suggesting that movements into the Chukchi Sea are rare, and coastal areas are not where ribbon seals feed. Their geographic range and remote distribution in the pack ice and the Bering Sea shelf (Braham et al. 1984; Simpkins et al. 2003) are consistent with these findings. Ribbon seals reside in the Bering Sea during the ice-free months and few are seen or harvested north of the Bering Strait in Alaska (reviewed in Boveng et al. 2008).

Interannual variability of stable isotope ratios in claws indicates ice seals are versatile predators that are able to adjust to changing food sources depending on availability. The extremely low minimum summer sea ice extent for five consecutive years occurred from 2007 through 2011, with 2007 having the record low sea ice extent in the Arctic (NSIDC 2011a). Standardized residuals of $\delta^{15}N$ values for ringed seal claws decreased during 2007, and this may be related to less sea ice in that year and its effects on food-web structure. Less sea ice and earlier ice melt is predicted to result in a more pelagic-dominated food web rather than the current more benthic-dominated food web (Bluhm and Gradinger 2008). The expansion and longer duration of open water period in the Arctic led to an increase in annual primary production in 2007 relative to 2006 (Arrigo et al. 2008). Ultimately, elevated primary production, early ice retreat coupled with warmer waters (NSIDC 2011a), and a longer open water season may support a higher abundance of pelagic crustacean grazers (Hunt and Stabeno 2002) that can then be consumed by ice seals. $\delta^{15}N$ values indicating that ringed seals were feeding at a lower trophic level in 2007 (Figure 3.3a) may be due to a greater availability of pelagic crustaceans. Ringed seals are known to consume dense swarms of euphausiids and

amphipods during summer and early autumn (Lowry et al. 1980a). Sea ice extent was relatively low from 2008 to 2010, compared to the median from 1979 through 2000 (NSIDC 2011a); however, $\delta^{15}N$ values in ringed seal claws after 2008 indicated they were feeding at a higher trophic level. Fish abundance may also increase in response to an increase in the biomass of zooplankton (Overland and Stabeno 2004; Grebmeier et al. 2006). A decrease in $\delta^{13}C$ values of ringed seal claws from 1998 to 2010 (Figure 3.5b) may be a result of a decrease in sea ice extent in the Arctic. Between 1998 and 2007, there was a decrease in the 12–month running mean in sea ice extent with an increase after 2008 before decreasing again (NSIDC 2011b). A decrease in sea ice reduces the area available for ice algae to grow, which may result in less biomass of ice algae to support secondary consumers (Carroll and Carroll 2003). In turn, zooplankton may transition from foraging under the sea ice to foraging more pelagically leading to these secondary consumers and higher trophic level predators having lower $\delta^{13}C$ values, i.e., phytoplankton are more deplete in ^{13}C relative to ice algae (Gradinger 2008). Overall, interannual trends in trophic level foraging suggest that ringed seals are flexible to climate change impacts on trophodynamics.

For bearded seal claws, a decrease in $\delta^{15}N$ values during 2007 and lower $\delta^{13}C$ values after 2007 may provide support for more pelagic feeding in years of low sea ice cover. Lower trophic level foraging in 2007 may be a result of bearded seals consuming bivalves. Alternatively, these seals may have been consuming a higher proportion of pelagic crustaceans similar to ringed seals. For example, euphausiids (*Thysanoessa* spp.) and ampipods (e.g., *Gammarus* spp.) are prey items commonly identified in both ringed

and bearded seal stomachs (Johnson et al. 1966; Quakenbush et al. 2010a, b). However, these species may be found throughout the water column (euphausiids; ArcOD 2010) and are associated with the sea-ice and sea-bottom (e.g., *Gammarus wilkitzkii*; Arndt et al. 2005). Zooplankton feeding under the ice or near the sea floor may have similar carbon isotope signatures because ice algae trapped in brine channels exhibit similar ^{13}C enrichment as algae in the benthos (Kennedy et al. 2002). Pelagic zooplankton typically are deplete in ^{13}C relative to benthic consumers or zooplankton grazing on ice algae (McConnaughey and McRoy 1979; Kennedy et al. 2002). A trend of decreasing $\delta^{13}C$ values from 2008 to 2010 (Figure 3.7b) may provide support for bearded seals foraging more pelagically over time due to a decrease in benthic biomass. Benthic biomass is dependent on the quality and quantity of food reaching the benthos (Grebmeier et al. 1988). A decrease in benthic biomass may gradually occur over time, but it is likely on a scale of several years (Dunton et al. 2005). Thus, an overall response of bearded seals feeding more pelagically may not be as immediate. Inferences regarding an increase in pelagic foraging for bearded seals should be interpreted with caution as mean $\delta^{13}C$ values may be biased by the relatively small sample size of claws having stable isotope data after spring/summer 2008. Ultimately, stable isotope signatures in claws may provide evidence of an increase in pelagic foraging for bearded seals; however, the use of stable isotopes to track these changes may not be ideal due to regional variations in carbon source as discussed above.

While an interannual trend was not apparent when assessing standardized residuals for $\delta^{15}N$ values of spotted seal claws, during 2006 spotted seals may have

consumed lower trophic level prey. About 70% of the spotted seal pups born in 2006 had lower $\delta^{15}N$ values compared to seals born in 2007 and 2008 (Figure 3.8a). This indicates differences in maternal trophic level and nutrient transfer to the pup. In addition, two adult spotted seals also fed lower trophically in fall/winter 2006, suggesting a response to changes in the Arctic food web. Although, summer sea ice extent in the Arctic has been relatively low from 2007 through 2011, the winter sea ice extent in the Bering Sea was greater than average during the winter 2012, i.e., second highest sea ice extent in January compared to averages from 1979–2000 (NSIDC 2012). Moreover, ocean temperatures in the Bering Sea were colder from winter 2006 to winter 2009 compared to 2000 through 2005 (Overland et al. 2009). Colder temperatures may have allowed for Arctic species to extend their range into sub-Arctic waters (Grebmeier et al. 2006); thus, more secondary consumers may have been available for consumption by spotted seals. However, sample size is small and lower trophic foraging during fall/winter 2006 may be a result of prey preference by individual seals or local variation in food sources. Overall, high variability of diets within the seal populations confounds the variation explained by temporal effects (Table 3.3). This further demonstrates the potential and ability of ice seal populations to adjust to changes in food-web structure in the Arctic.

Examining other tissues and additional investigations (i.e., using archived claws to reach further back in time, such as capturing the regime shift in the late 1970s; Hare and Mantua 2000) using stable isotopic signatures of claws could aid in describing the diet strategies of ice seals and food chain effects. For processing of growth bands, claws should be soaked until the ungual crest can be loosened from the quick. The two to three

growth bands underneath the ungual crest are essential for minimum age estimates and consequent stable isotope analysis. The seasonal resolution using stable isotope signatures in claw growth bands is low as each band represents an integrated isotopic signature over several months. Future studies may be able to provide better insight into seasonal changes of ice seal diets by using micro drills to process each growth band at 300 μm intervals (Newsome et al. 2010). Furthermore, a combination of whisker and claw stable isotope analysis could improve the seasonal resolution (Cherel et al. 2009), as whiskers have relatively faster growth rates (Zhao and Schell 2004), while simultaneously documenting interannual differences in diet over time. Understanding diet alterations for a predator with a varied diet and a wide geographic range complicates interpretations when using an integrated descriptor such as stable isotope ratios. Ultimately, stable isotopes are not a replacement for stomach content analysis, but are a valuable supplemental tool to enhance our understanding of integrated seasonal or interannual feeding ecology of ice seals.

Claws provide a unique glimpse into the foraging history of ice seals. In addition to providing dietary information at the population level, similar to long-term studies examining stomach contents (Quakenbush et al. 2009, 2010a, b), claws also describe the long-term diet of individuals. The variability among individuals and interannual variations in diet documented in this study exemplifies the opportunistic nature of ringed, bearded, spotted, and ribbon seals and their adaptation potential to changes in food-web structure in the Arctic.

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TABLES

Table 3.1. Inventory of Claws Collected from Ice Seals. Ice seal claws analyzed for stable nitrogen and carbon isotope ratios. The asterisk marks the individual ringed seal where all 5 claws were analyzed from one front flipper. Some seal tooth ages are still to be determined (TBD).

	Location	Year	Month	Base Band	Tooth Age Est.	Claw Age Est.	Sex
Ringed Seals							
	Point Hope	2010	February	Dark	10	8.5 +	Male
	Hooper Bay	2010	February	Dark	13	11.5	Female
	Hooper Bay	2010	February	Dark	20	11.5 +	Male
	Barrow	2010	March	Dark	N/A	8 +	Unknown
	Barrow	2010	March	Dark	N/A	11.5 +	Female
	Barrow	2010	March	Dark	N/A	11.5 +	Unknown
	Point Hope	2009	June	Light	8	8	Male
	Barrow	2008	July	Light	TBD	9 +	Female
	Barrow	2009	July	Light	18	9 +	Male
	Point Hope	2010	July	Light	21	8 +	Male
	Point Hope	2010	July	Light	37	10 +	Male
	Barrow	2010	July	Light	TBD	7	Male
	Barrow	2010	July	Light	TBD	12 +	Female
	Barrow	2008	August	Dark	TBD	7.5 +	Female
*	Barrow	2011	September	Dark	N/A	9+	Male
	Shishmaref	2009	October	Dark	4	4	Unknown
	Shishmaref	2009	October	Dark	8	6 +	Male
	Shishmaref	2009	October	Dark	10	8.5 +	Male
Bearded Seals							
	Little Diomede	2009	May	Light	5	5	Male
	Point Hope	2009	June	Light	7	7	Female
	Point Hope	2010	June	Light	11	10 +	Female
	Barrow	2010	June	Light	TBD	10 +	Unknown
	Point Hope	2010	June	Light	20	11 +	Unknown
	Barrow	2010	June	Light	TBD	11 +	Male
	Barrow	2010	June	Light	TBD	8 +	Male
	Barrow	2008	July	Light	TBD	4	Male
	Barrow	2008	July	Light	TBD	4	Male
	Barrow	2008	July	Light	TBD	5	Unknown
	Barrow	2008	July	Light	TBD	5	Unknown
	Barrow	2008	July	Light	N/A	5	Unknown
	Barrow	2008	July	Light	TBD	7 +	Female
	Barrow	2010	July	Light	TBD	8 +	Male
	Barrow	2008	July	Light	TBD	9 +	Male
	Barrow	2008	July	Light	N/A	10 +	Male

Table 3.1 Inventory of Claws Collected from Ice Seals (continued). Ice seal claws analyzed for stable nitrogen and carbon isotope ratios. The asterisk marks the individual ringed seal where all 5 claws were analyzed from one front flipper. Some seal tooth ages are still to be determined (TBD).

	Location	Year	Month	Base Band	Tooth Age Est.	Claw Age Est.	Sex
Spotted Seals							
	Barrow	2009	July	Light	8	7 +	Unknown
	Shishmaref	2009	September	Dark	3	3	Male
	Shishmaref	2009	September	Dark	N/A	3	Male
	Shishmaref	2009	September	Dark	6	6	Male
	Shishmaref	2009	October	Dark	1	1	Female
	Shishmaref	2009	October	Dark	1	1	Female
	Shishmaref	2009	October	Dark	1	1	Male
	Shishmaref	2009	October	Dark	TBD	1	Female
	Shishmaref	2009	October	Dark	2	2	Male
	Shishmaref	2009	October	Dark	TBD	2	Male
	Shishmaref	2009	October	Dark	TBD	2	Unknown
	Shishmaref	2009	October	Dark	3	3	Female
	Shishmaref	2009	October	Dark	3	3	Male
	Shishmaref	2009	October	Dark	TBD	3	Female
	Shishmaref	2009	October	Dark	TBD	3	Female
	Shishmaref	2009	October	Dark	TBD	3	Female
	Shishmaref	2009	October	Dark	4	4	Male
	Shishmaref	2009	October	Dark	5	5	Male
	Shishmaref	2009	October	Dark	TBD	5	Unknown
	Shishmaref	2009	October	Dark	TBD	7.5 +	Female
Ribbon Seals							
	Hooper Bay	2010	February	Dark	8	8.5 +	Male
	Hooper Bay	2010	February	Dark	11	9.5 +	Female
	Point Hope	2007	June	Light	13	12 +	Female

Table 3.2 Correlation of Stable Isotope Signatures Between Digits. Pearson's correlation *p*-value describing correlation for stable nitrogen and carbon isotope ratios among all 5 claws (Digit I–V) from a ringed seal front flipper.

Nitrogen					
	Digit I	Digit II	Digit III	Digit IV	Digit V
Digit I					
Digit II	< 0.001				
Digit III	< 0.001	< 0.001			
Digit IV	< 0.001	< 0.001	< 0.001		
Digit V	< 0.001	< 0.001	0.009	< 0.001	

Carbon					
	Digit I	Digit II	Digit III	Digit IV	Digit V
Digit I					
Digit II	< 0.001				
Digit III	< 0.001	< 0.001			
Digit IV	< 0.001	< 0.001	< 0.001		
Digit V	< 0.001	< 0.001	0.002	< 0.001	

Table 3.3 Variation Among Seals and Time. Total percent contribution of variance among individuals, time, and residual error for ringed, bearded, and spotted seals.

Source of Variance	Ringed Seal		Bearded Seal		Spotted Seal	
	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$
Among Individuals	59.1	75.9	73.8	91.1	71.7	65.0
Time	0.1	0.1	0.4	0.1	0.4	0.4
Residual	40.8	23.9	25.8	8.8	27.9	34.7

FIGURES

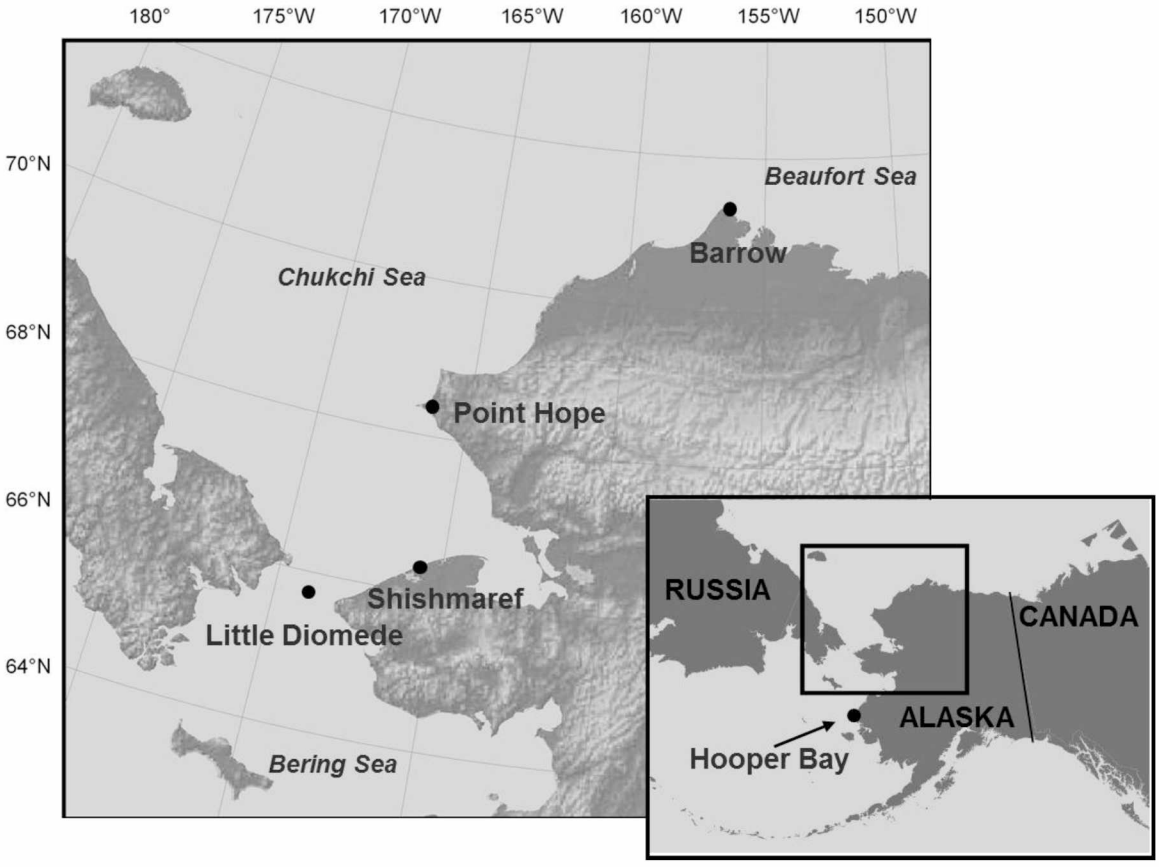

Figure 3.1 Sample Collection Map. Location map of Alaska Native subsistence communities where claws of ice seals were collected.

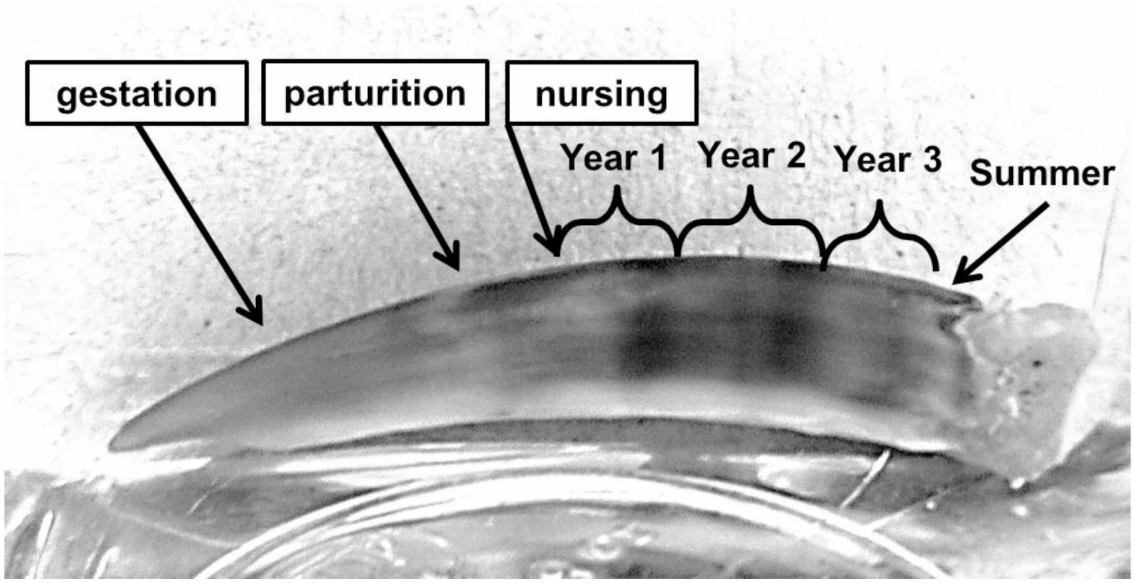

Figure 3.2 Seal Claw Photo Description. Claw of a 3-year-old spotted seal. Each year consists of a light (spring/summer) and dark (fall/winter) band. The base of the claw represents the most recent growth and the tip is the oldest growth. Labels indicate drilling locations to assess stable nitrogen and carbon isotope ratios for pre-natal growth (gestation), constriction region/natal notch (parturition), and post-natal growth (nursing).

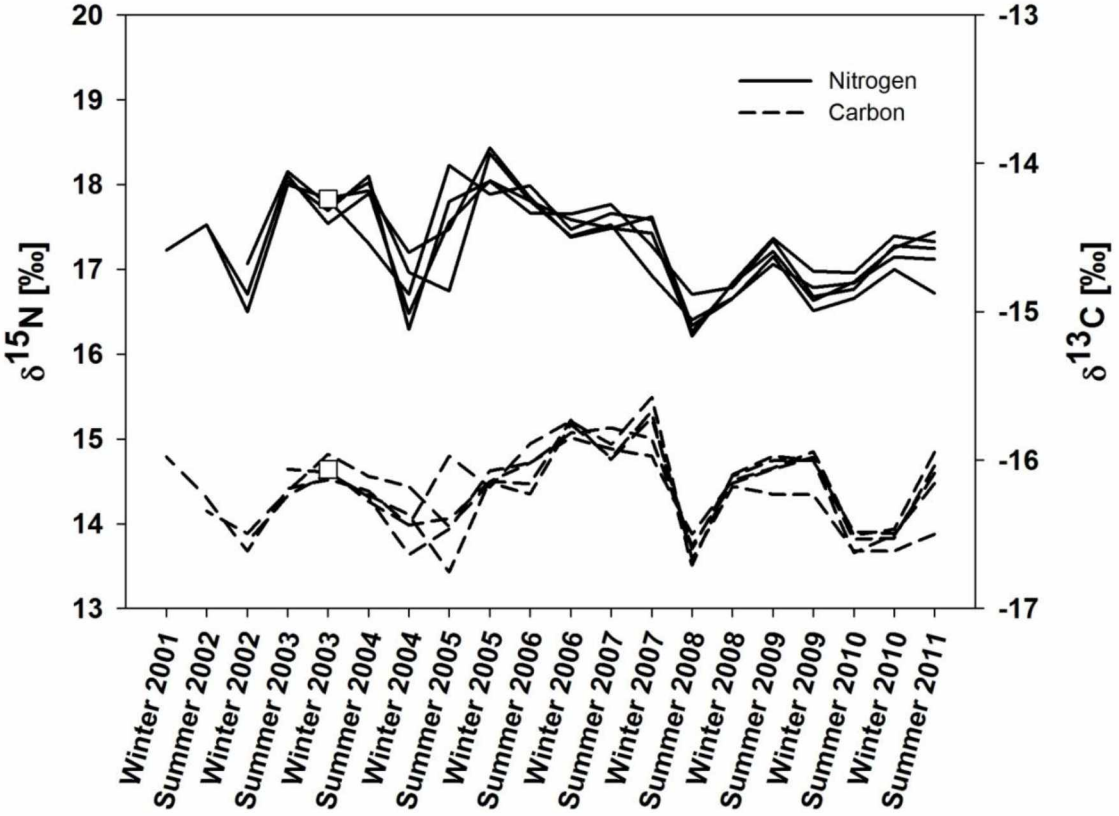

Figure 3.3 Variation Among Digits. Stable nitrogen (solid line) and carbon (dashed line) isotope ratios for seasonal growth bands of all 5 claws (Digits I–V) from a ringed seal front flipper. White square symbol marks the last growth band present from Digit V.

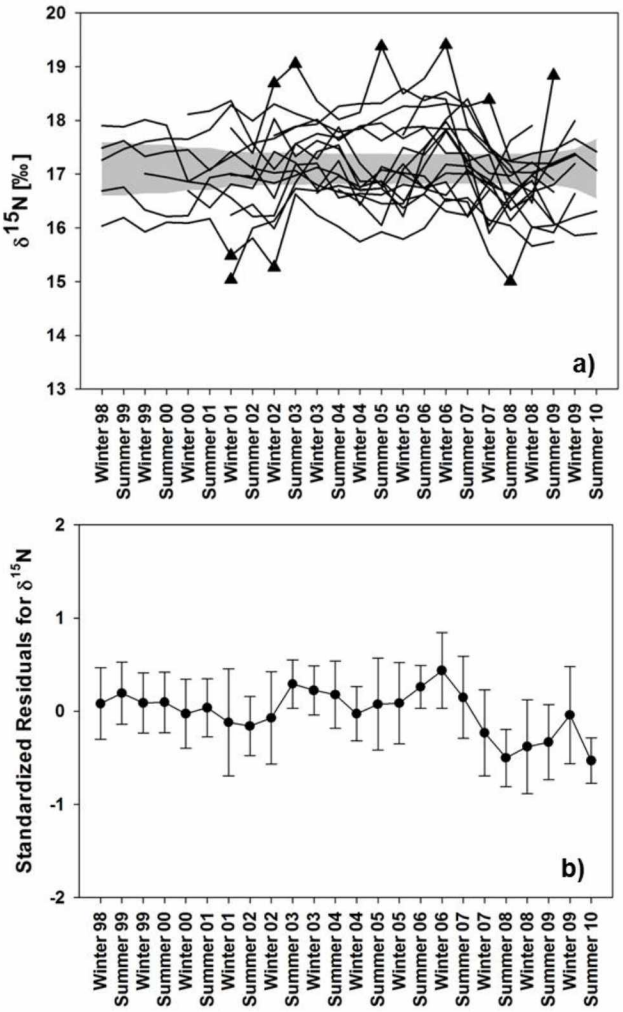

Figure 3.4 δ^{15}N values for Ringed Seal Claws. A) δ^{15}N values for seasonal growth bands of ringed seal claws. The gray region shows 95% confidence limits created using a mixed-effects model. Triangles are "anomalies" based on studentized residuals greater than 2. **B)** Standardized residuals for δ^{15}N values in seasonal growth bands of ringed seal claws. Isotope values were normalized to the mean of each individual and error bars display the standard deviation among seals. For seasonal bands (x-axis), winter corresponds to trophic position of seals during fall/winter, while summer describes trophic level during spring/summer.

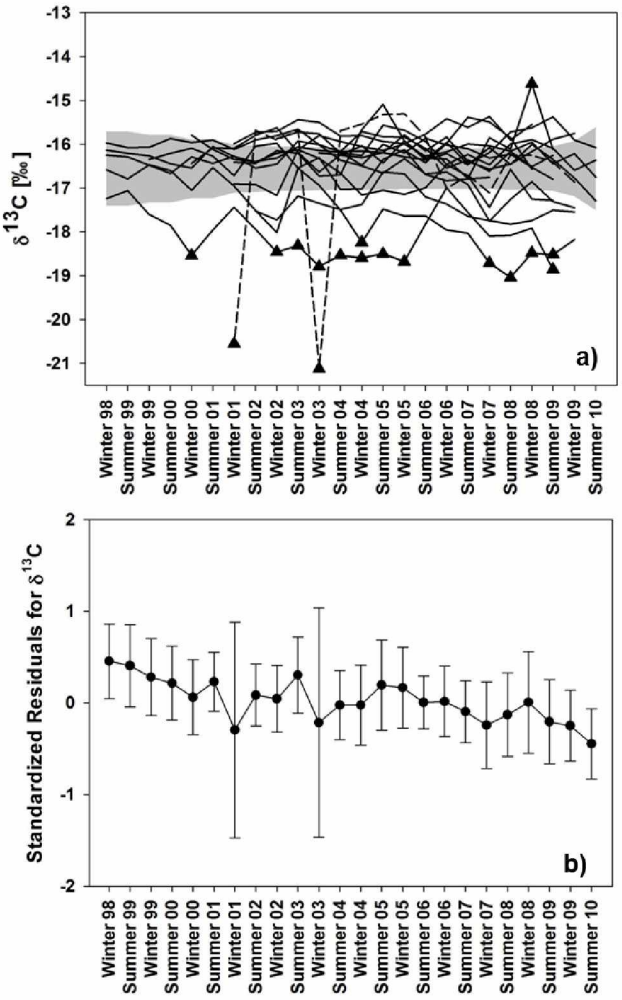

Figure 3.5 $\delta^{13}C$ values for Ringed Seal Claws. A) $\delta^{13}C$ values for seasonal growth bands of ringed seal claws. The gray region shows 95% confidence limits created using a mixed-effects model. Triangles are "anomalies" based on studentized residuals greater than 2. **B)** Standardized residuals for $\delta^{13}C$ values in seasonal growth bands of ringed seal claws. Isotope values were normalized to the mean of each individual and error bars display the standard deviation among seals. For seasonal bands (x-axis), winter corresponds to trophic position of seals during fall/winter, while summer describes trophic level during spring/summer.

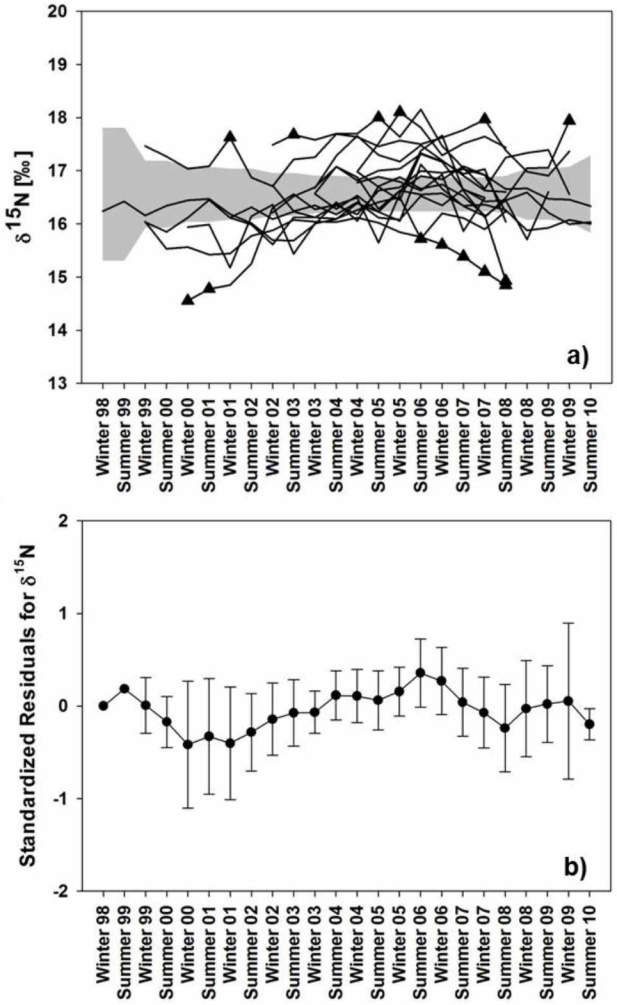

Figure 3.6 δ^{15}N values for Bearded Seal Claws. A) δ^{15}N values for seasonal growth bands of bearded seal claws. The gray region shows 95% confidence limits created using a mixed-effects model. Triangles are "anomalies" based on studentized residuals greater than 2. **B)** Standardized residuals for δ^{15}N values in seasonal growth bands of bearded seal claws. Isotope values were normalized to the mean of each individual and error bars display the standard deviation among seals. For seasonal bands (x-axis), winter corresponds to trophic position of seals during fall/winter, while summer describes trophic level during spring/summer.

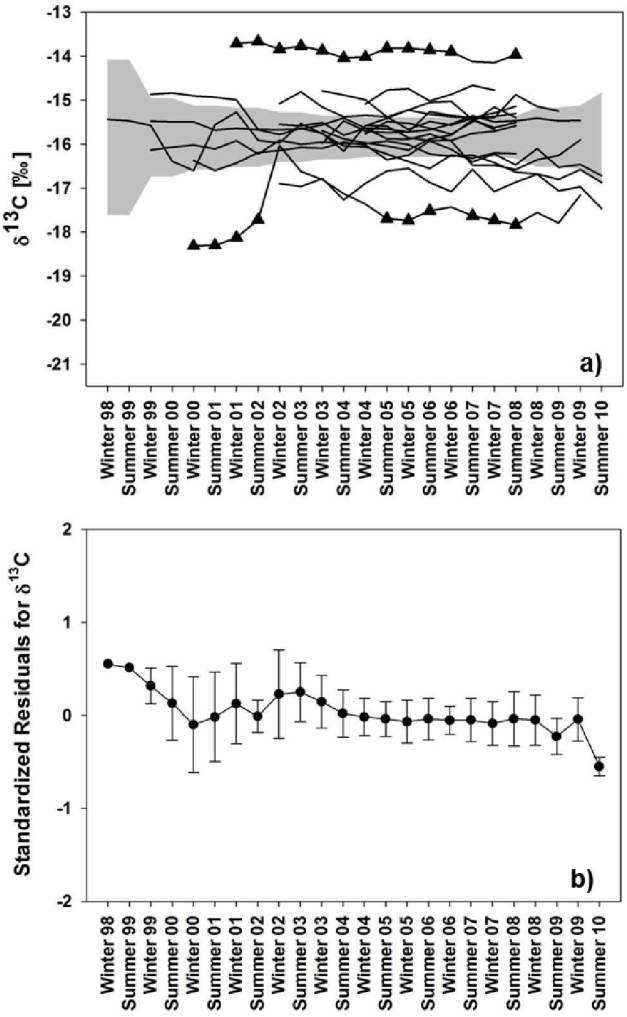

Figure 3.7 $\delta^{13}C$ values for Bearded Seal Claws. A) $\delta^{13}C$ values for seasonal growth bands of bearded seal claws. The gray region shows 95% confidence limits created using a mixed-effects model. Triangles are "anomalies" based on studentized residuals greater than 2. **B)** Standardized residuals for $\delta^{13}C$ values in seasonal growth bands of bearded seal claws. Isotope values were normalized to the mean of each individual and error bars display the standard deviation among seals. For seasonal bands (x-axis), winter corresponds to trophic position of seals during fall/winter, while summer describes trophic level during spring/summer.

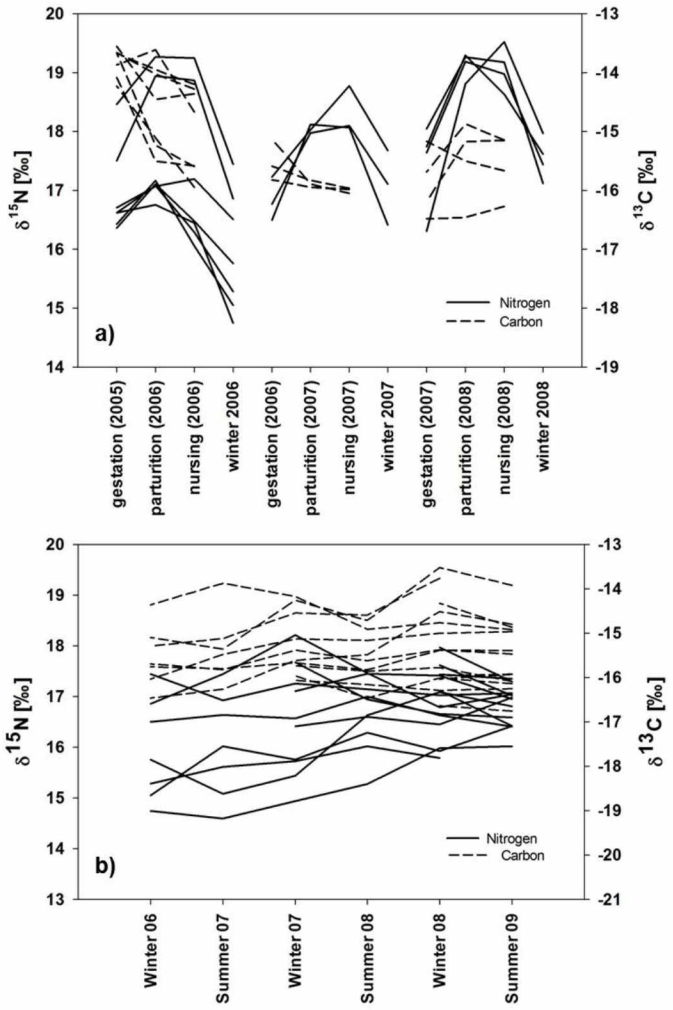

Figure 3.8 Stable Isotope Signatures for Young Spotted Seal Claws. Stable nitrogen (solid line) and carbon (dashed line) isotope ratios for seasonal growth bands of spotted seal claws (n = 14) ranging from one to three years of age. Isotope signatures recorded in claws during (**a**) fetal/pup developmental phases, i.e., gestation (tip of claw), parturition (natal notch), lactation (first light band after natal notch), and fall/winter foraging (first dark band after natal notch). A continuation of stable nitrogen and carbon isotope signatures recorded in claws during (**b**) juvenile development from first winter foraging until harvest in summer 2009.

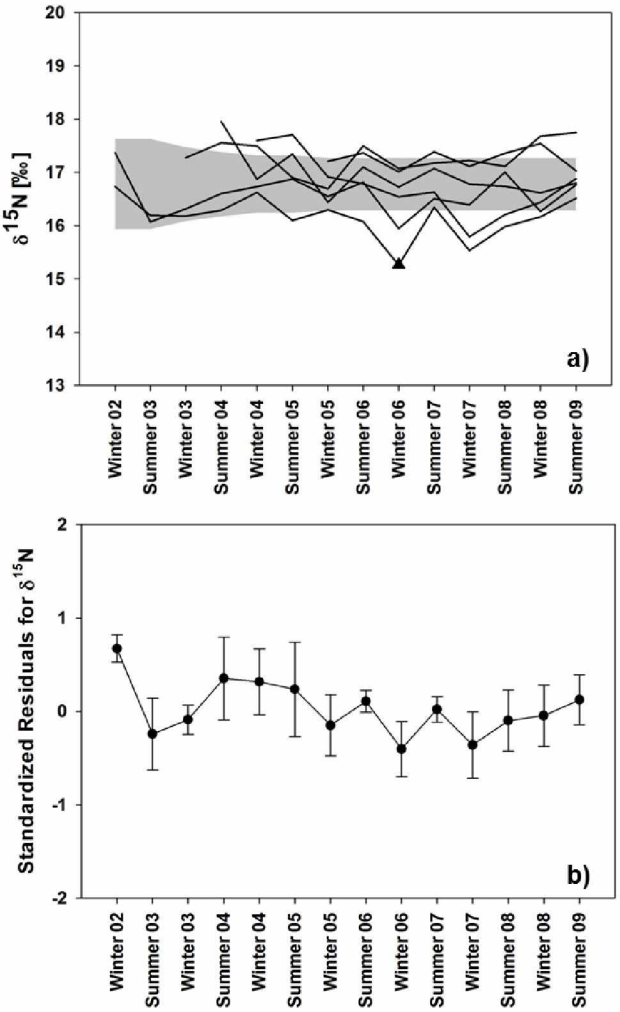

Figure 3.9 δ^{15}N values for Spotted Seal Claws. A) δ^{15}N values for seasonal growth bands of spotted seal claws. The gray region shows 95% confidence limits created using a mixed-effects model. Triangles are "anomalies" based on studentized residuals greater than 2. **B)** Standardized residuals for δ^{15}N values in seasonal growth bands of spotted seal claws. Isotope values were normalized to the mean of each individual and error bars display the standard deviation among seals. For seasonal bands (x-axis), winter corresponds to trophic position of seals during fall/winter, while summer describes trophic level during spring/summer.

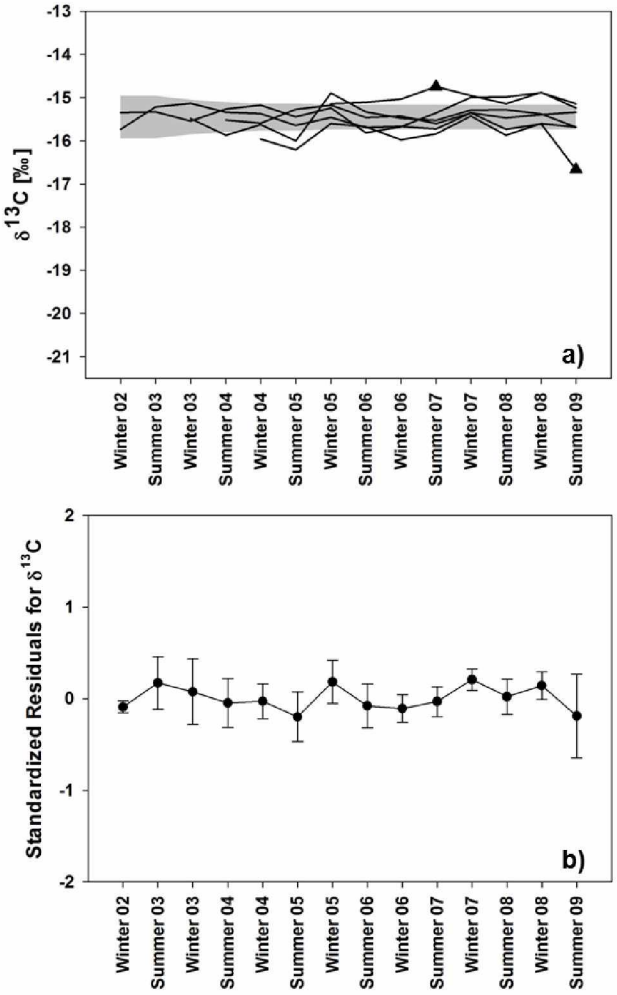

Figure 3.10 $\delta^{13}C$ values for Spotted Seal Claws. A) $\delta^{13}C$ values for seasonal growth bands of spotted seal claws. The gray region shows 95% confidence limits created using a mixed-effects model. Triangles are "anomalies" based on studentized residuals greater than 2. **B)** Standardized residuals for $\delta^{13}C$ values in seasonal growth bands of spotted seal claws. Isotope values were normalized to the mean of each individual and error bars display the standard deviation among seals. For seasonal bands (x-axis), winter corresponds to trophic position of seals during fall/winter, while summer describes trophic level during spring/summer.

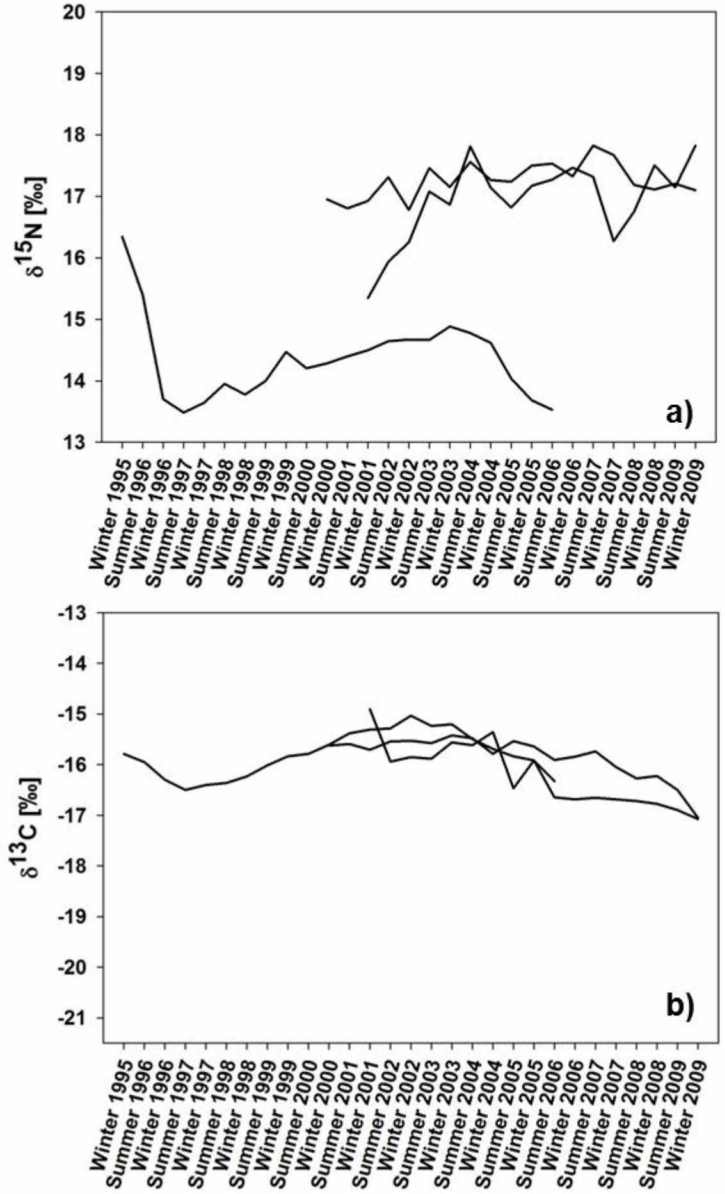

Figure 3.11 Stable Isotope Signatures for Ribbon Seal Claws. Stable nitrogen (**a**) and carbon (**b**) isotope ratios for seasonal growth bands of ribbon seal claws. For seasonal bands (x-axis), winter corresponds to trophic position of seals during fall/winter, while summer describes trophic level during spring/summer.

CHAPTER 4:

General Conclusion

During the initial years of record sea ice minima, i.e., 2007 and 2008 (NSIDC 2011), ringed seals fed lower trophically as described by stable isotope analysis of muscle and claws, and this is in agreement with my hypothesis. Muscle samples were not available from 2007. However, time series data recorded in claws showed the largest decrease in $\delta^{15}N$ values for the sampled population during 2007. Isotopic mixing model results for muscle showed a high proportional contribution of euphausiids, i.e., lower trophic crustaceans, to the diet of ringed seals during 2008 and 2009. After 2007, $\delta^{15}N$ values in claws gradually increased across the sampled population as some individuals continued foraging at a lower trophic level, while other seals began taking advantage of higher trophic level prey items. When examining stable isotope ratios of individual muscle samples, about 29% (8 or 28 seals) of the sampled population were feeding lower trophically in 2008 and 2009 combined (Figure 2.3c), while the other 71% fed at a higher trophic level. This high individual variation created a large range for the proportional contribution of lower trophic crustaceans to the diet of the sampled population, i.e., 0–30%. In general, the majority of ringed seals may have taken advantage of the higher biomass of lower trophic prey available during the record sea ice minimum extent of 2007. However, as the biomass of pelagic consumers increased individual seals likely began to take advantage of higher tropic level prey (Overland and Stabeno 2004; Grebmeier et al. 2006). Stable isotope analysis of both muscle and claws showed similar interannual trends along with high individual variation in the diet of ringed seals.

Based on stable isotope results for muscle and claws, it appears that as sea ice extent and thickness decreased, bearded seals may have been foraging more pelagically. Isotopic mixing model results for muscle showed a decrease in the range of proportional contribution for demersal fishes, while the range increased for pelagic fishes over time. Bivalves made up a larger contribution to diet in 2008–2010 compared to 2003; however, this prey guild represents lower trophic prey and isotopic mixing model results could also be showing an increase in foraging on pelagic crustaceans. An initial transition to pelagic foraging was also described for bearded seal claws as $\delta^{13}C$ values decreased after 2008; although, sample size was low after 2008. Bearded seals may be foraging more pelagically during low ice years as proposed in my hypothesis. However, a transition to pelagic foraging may be gradual and not immediately apparent for a sampled population of bearded seals as there would likely be a time lag before benthic biomass in the Arctic ecosystem decreased noticeably (Dunton et al. 2005), that is if sea ice continues to decline in extent and thickness in years to come. Thus, continued analysis and monitoring of ice seal diets is necessary. Overall, bearded seals have a varied diet, high individual variation, and a large geographic range possibly masking any temporal trends.

An interannual trend was not apparent when comparing stable isotope analysis of muscle and claws from spotted seals; however, results may provide evidence of these seals taking advantage of prey nearshore and under the sea ice in the Bering and Chukchi Seas. Analysis of claws showed lower trophic foraging during 2006 and this contrasts my hypothesis as I expected lower trophic foraging to occur during 2007. However, sample size of adult claws was low and a larger sample size is necessary to provide support to

interannual trends. Unfortunately, muscle samples were not available for 2006; therefore, a comparison could not be made to compare if observed trends matched between tissues. Isotopic mixing model results for muscle documented regional differences in foraging; in 2009 more seals seemed to feed nearshore on smelt compared to 2008. When examining stable isotope ratios in muscle across individual samples from 2009, there was a wide range of carbon isotope signatures with some tissues being enriched in ^{13}C, while others were more depleted in ^{13}C, i.e., similar to isotope signatures of smelt. However, tissues depleted in ^{13}C may be a result of foraging offshore as nearshore regions are typically more enriched in ^{13}C (reviewed in Newsome et al. 2010). Conclusions based on isotopic mixing model results may thus be completely opposed as seals in 2008 may have been foraging more nearshore, while some individuals were feeding offshore in 2009. Great care should be taken when interpreting mixing model results of tissues with long metabolic turnover times as regional differences may confound isotopic signatures resulting in contrasting scenarios. Generally, there was high individual variation across muscle samples of spotted seals. Claws were enriched in ^{13}C and showed little variation for carbon signatures during the recorded time series, and it is likely that subadults and adults were foraging nearshore in the summer and feeding under the sea ice in the winter, i.e., prey from both areas being enriched in ^{13}C (Kennedy et al. 2002; Newsome et al. 2010). Ultimately, regional differences in carbon isotopes may mask the distinct isotope signature of prey items and potentially lead to misrepresenting conclusions.

Interannual trends were not examined for ribbon seals as only few claw samples were available; however, general diet was inferred for three individuals. There is some

indication that $\delta^{15}N$ values increase with age, so higher trophic prey may increase in importance later in life (Fedoseev 2000; Dehn et al. 2007). $\delta^{13}C$ values in ribbon seal claws were stable with little variation among individuals, seasons, or years. This illustrates foraging at remote locations near the shelf break in the Bering Sea consistent with their life history (Boveng et al. 2008).

Stable isotope analysis of muscle and claws is a useful tool to assess interannual trends, but this tool should be paired with other forms of analysis to provide additional insights. Conclusions from isotopic mixing models should be interpreted with caution as this tool may not be useful in describing contributions of particular prey items to the diet of ice seals. Ice seals have varied diets and large geographic range that differ isotopically. For instance, the higher contribution of smelt to ringed seal diets in 2003 and 2010 may have been a result of seals foraging in a region more depleted in ^{13}C, such as the Beaufort Sea compared the to the Chukchi Sea (Dunton et al. 2006). However, this tool can be beneficial in assessing interannual trends, e.g., lower trophic foraging for ringed seals during ice minimum years. Ice seal claws offer a unique glimpse into the diet history of individuals and highlight foraging trends for the sampled population when time series are compared. Dietary time series data recorded within claws can be processed over a short period of time, i.e., two months to drill 56 claws for this study. In contrast, the manpower needed to produce the same amount of information to document an interannual trend of ice seal diet by compiling stomach content data would take years and a large amount of samples, e.g., 56 stomachs over 10 years totaling to 560 samples. However, stable isotope analysis of claws does not replace the information obtained from stomach contents

describing diet at a much higher taxonomic resolution. Comparing changes in prey species across decades using stomach content analysis (Quakenbush et al. 2009, 2010a, b) as well as interannual trends documented using stable isotope analysis of claws would enhance understanding of the feeding ecologies of ice seals and their ability to adapt to changes in food-web structure.

This thesis documented high individual variation in the diet of Arctic ice seals. Temporal trends illustrated ice seals taking advantage of abundant prey sources during the ice minima year of 2007. Ultimately, ice seals are opportunistic predators and likely resilient to climate change effects on trophodynamics.

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